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The termites of South-east Asia : a study of biogeographical patterns

Gathorne-Hardy, Frederick Jasper

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THE TERMITES OF SOUTHEAST ASIA: A STUDY OF BIOGEOGRAPHICAL PATTERNS

by

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A thesis submitted for the degree of Doctor of Philosophy of the University of London

March 2002

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To my parents

ABSTRACT

This thesis has four main aims: 1. To survey the termites of the Sunda region taxonomically and ecologically (much of which has never been surveyed), 2. To investigate diversity patterns within the region, 3. To investigate the effects of Quaternary climate change on termites, and 4. To investigate the effects of human disturbance on termite assemblages.

The ecological survey work was mostly carried out using a standardised transect sampling technique, which has been demonstrated to be effective. In order to overcome taxonomic problems, I have revised the soil-feeding Nasutitermitinae and have synonomised a number of species in other subfamilies.

I found that on Sulawesi, there was an unusually low number of soil-nesting species of termite, when compared to the Sunda shelf. This shows that, even after millions of years, most termite species cannot cross water gaps. Work in the Leuser Ecosystem shows that termite species richness and relative abundance decline with even a hundred metre increase in altitude, and differences in mean annual rainfall may also have an effect on the termite assemblage.

I found that present day differences in termite composition across Southeast Asia can be explained as a product of Quaternary climate change, and that modern termite assemblages can be used to indicate the extent of this change. I used a combination of present termite assemblage distributions, palynological, geological and fossil data to map the extent of the savannah vegetation during the Last Glacial Maximum. At that time rainforest refugia were probably present in northern and eastern Borneo, northern and western Sumatra and the Mentawai islands, while the rest of the region was probably covered by savannah.

I show that high levels of rainforest disturbance cause a great reduction in termite species richness and abundance, as well as a dramatic change in composition. Recovery of the termites (and their vital ecosystem services) from large scale, severe disturbance is likely to take millenia.

Keywords: Borneo – Sumatra – Java – Sulawesi – Indonesia – Malaysia – conservation – colonisation – Quaternary – climate – refugia – rainforest.

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I would like to thank my parents for their prolonged support and encouragement while I have been writing this thesis. I am very grateful to Paul Eggleton for his advice and support, without which this thesis would never have been written. Peter Moore has helpfully proof-read my work, and provided administrative support at King's College. All of this work has benefited greatly from numerous discussions with David Jones, Sarah Donovan and Richard Davies. They have also proof-read much of the thesis and have provided much extremely useful advice. I am also grateful to Gathorne Cranbrook, Daegan Inward, Peter Hammond, Mark Collins, Pat Wolseley, Andy Current, John Proctor, Nick Mawdsley, Douglas Brandon-Jones, Helen Chaterjee for discussion, proof-reading and advice.

Mark Collins, Roger Buxton, Syaukani, Hasballah, Sugesti, Anggoro Prasetyo, Francis Susilo, David Jones, David Bignell and Paul Eggleton have all helped to collect termites or have made their termite collections available to me. Bill Sands, Anggoro Prasetyo and Luc Dibog provided taxonomic help and I am very grateful to Laurence Kirton and Sarkawi Hj. Mahammad Umar for allowing me to examine the termite collections at F.R.I.M. and the Forest Research Centre, Kuching.

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This project has been funded by the Leuser Development Programme, the Godman Fund, The Natural History Museum and free flights were provided by BA as part of its Assisting Conservation Scheme. Most of the funding has come from Hugh Gathorne-Hardy, however, for which I am extremely grateful.

Last but not least I would like to thank Mabintu Mustapha, for her support, hospitality and encouragement throughout the past 15 months.

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DECLARATION

The material submitted in this thesis is my own original research, except for the following parts:

Chapter 2: The termites were collected by N.M. Collins and R.D. Buxton. I identified the termites, prepared the figures and wrote the entire text.

Chapter 3: I collected the termites with the help of Syaukani, Hasballah and Sugesti. I identified two thirds of the specimens, and Syaukani identified the rest. I wrote the entire text, carried out the statistical analyses and prepared the figures.

Chapter 4: I wrote the text, made the keys and drew most of the illustrations. Sarah Donovan drew the guts of *Sabahitermes leuserensis*. Peter York photographed the enteric valves and the mandibles. I prepared all of the slides except for that of *Sabahitermes leuserensis*, which was prepared by Luc Dibog.

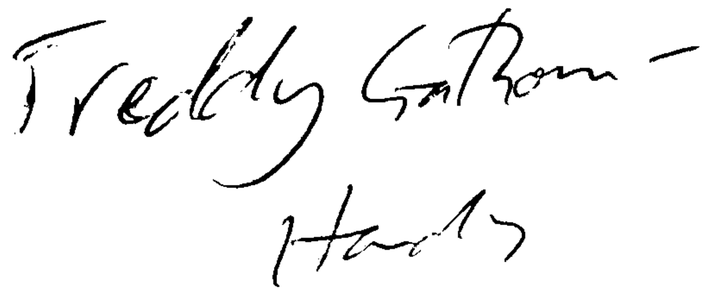
Chapter 5: I collected the termites from Siberut, Bukit Barisan National Park, Barito Ulu and Gunung Palung National Park with help from Syaukani. I identified all of the specimens which we collected. Termite data from other locations were provided by Richard Davies, Paul Eggleton and David Jones. I carried out the statistical analyses, prepared the figures and wrote the whole text.

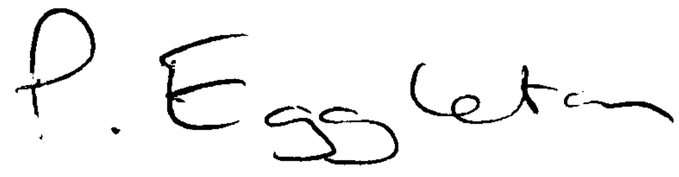
Chapter 6: I carried out the statistical analyses, prepared the figures and wrote the whole text. Additional termite data were provided by David Jones.

Frederick Gathorne-Hardy

Paul Eggleton

(Natural History Museum Supervisor)





INTRODUCTION

1.1 Background

The aim of this project is to try to understand the biogeography of the termites of Southeast Asia, focussing on Sundaland. I aim particularly to understand the effects of historical, ecological, geographical and human processes on termite assemblages.

Termites are the most important arthropod decomposers in tropical rainforests (Collins 1983, 1989; Wood & Sands 1978) and are vital for maintaining decomposition processes (Collins 1989, Wood 1988) and nitrogen and carbon cycles (Tayasu *et al.* 1997). They are thought to be a key source of soil heterogeneity (Donovan *et al.* 2001) and are at their highest diversity in lowland tropical rainforest (Collins 1989, Eggleton 2000). They are also a valuable food source for ants, birds, orang-utans, pangolins and other animals (Collins 1989).

Though I discuss all of Southeast Asia in this thesis, I will primarily be concerned with the Sunda region (or Sundaland). This includes the Malay Peninsula (up to the isthmus of Kra), Borneo, Sumatra, Java and surrounding islands. For most of history, the islands have been joined to the mainland, so they have a very similar flora and fauna. The region is clearly defined climatologically to the north (the climate becomes more seasonal north of the Kra isthmus), and geologically to the east (deep trenches-such as those below the Makassar and Lombok straits-divide Sundaland from Wallacea). Sundaland has been recognised as a biodiversity hotspot, about 5% of the world's plant species and 2.6% of the world's vertebrates are endemic to the region (Myers *et al.* 2000).

Sundaland is made up of many subcontinental blocks of Gondwanic origin. These spilt from Australia between the Early Carboniferous (340 Ma) and the late Jurassic (165 Ma), finally accreting to form proto-Sundaland in the late Cretaceous (80 Ma) (Metcalfe 1998).

It is unknown how much of Sundaland was above sea level until about 30 Ma, when most of it was exposed. In the early and middle Miocene a rise in sea levels covered almost all of what is now Sumatra (except for a few volcanic islands along the Barisan range). At the end of the Miocene more land became emergent and Java appeared for the first time. The Mentawai islands probably arose in the Pliocene (Samuel *et al.* 1997). By the Pliocene, most of the Sunda shelf had taken its present form and the majority of what are now islands were exposed (Hall 1998).

There was no major geological change in South East Asia during the Quaternary, though many minor ones, as the region is highly volcanic. Perhaps the most important of the volcanic eruptions of the Quaternary was the super-eruption of Toba, c. 73,500 (±2000) years ago (Chesner *et al.* 1991), which produced 2500-3000 km^3 of magma (dense rock equivalent) and probably injected at least 10^{15}g of fine ash into the stratosphere (Rampino & Self, 1993, Zielinski *et al* 1996, Bühring & Sarnthein, 2000). Pyroclastic flows covered about 10^5 km^2 (Rampino & Self, 1993) with lava reaching both the Malacca straits and the Indian Ocean (Rose & Chesner, 1987). Layers of ash, identified as Toba tuff, have been found in India, more than 3000 km away from Toba and in the South China Sea (Bühring & Sarnthein, 2000).

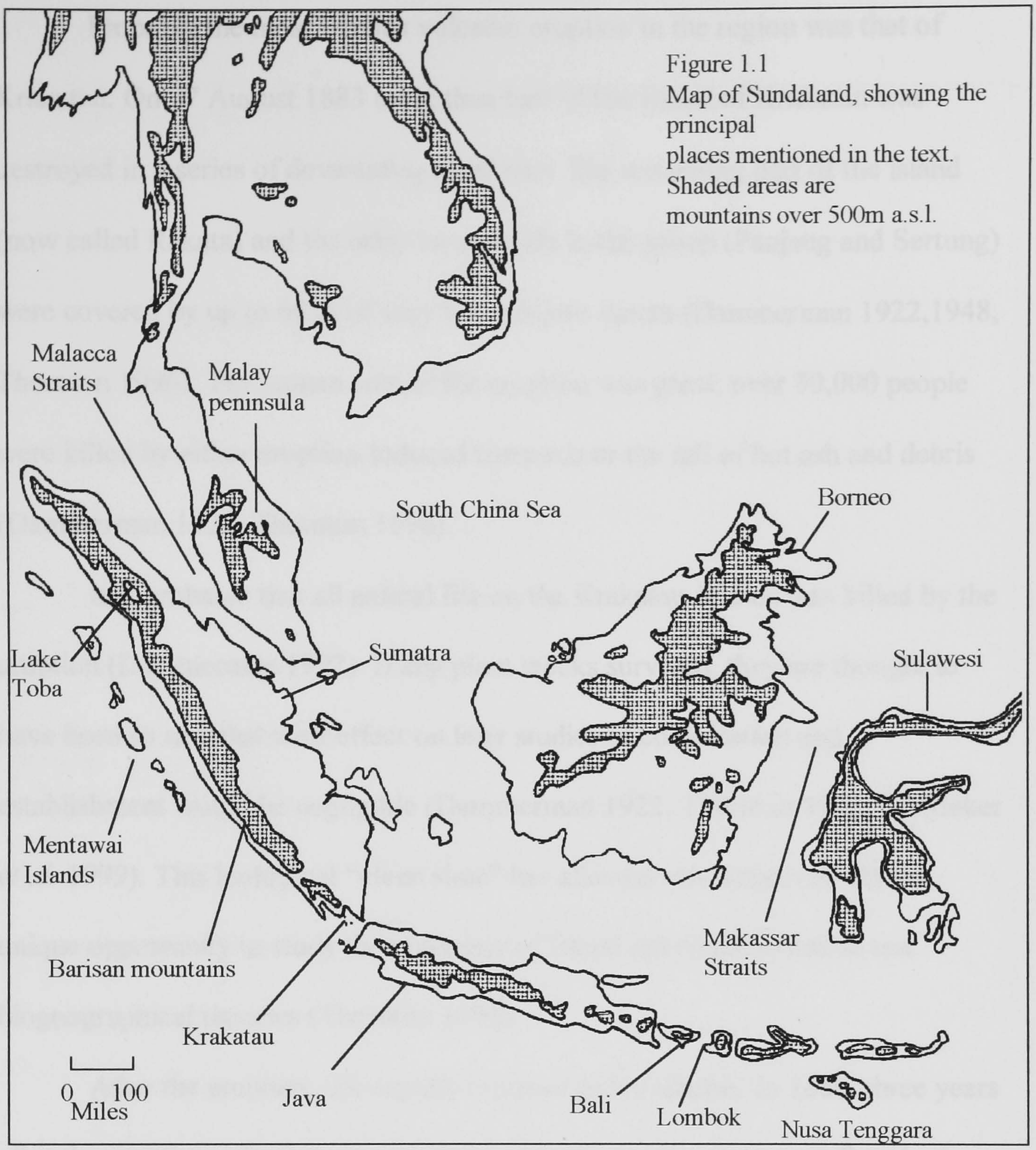


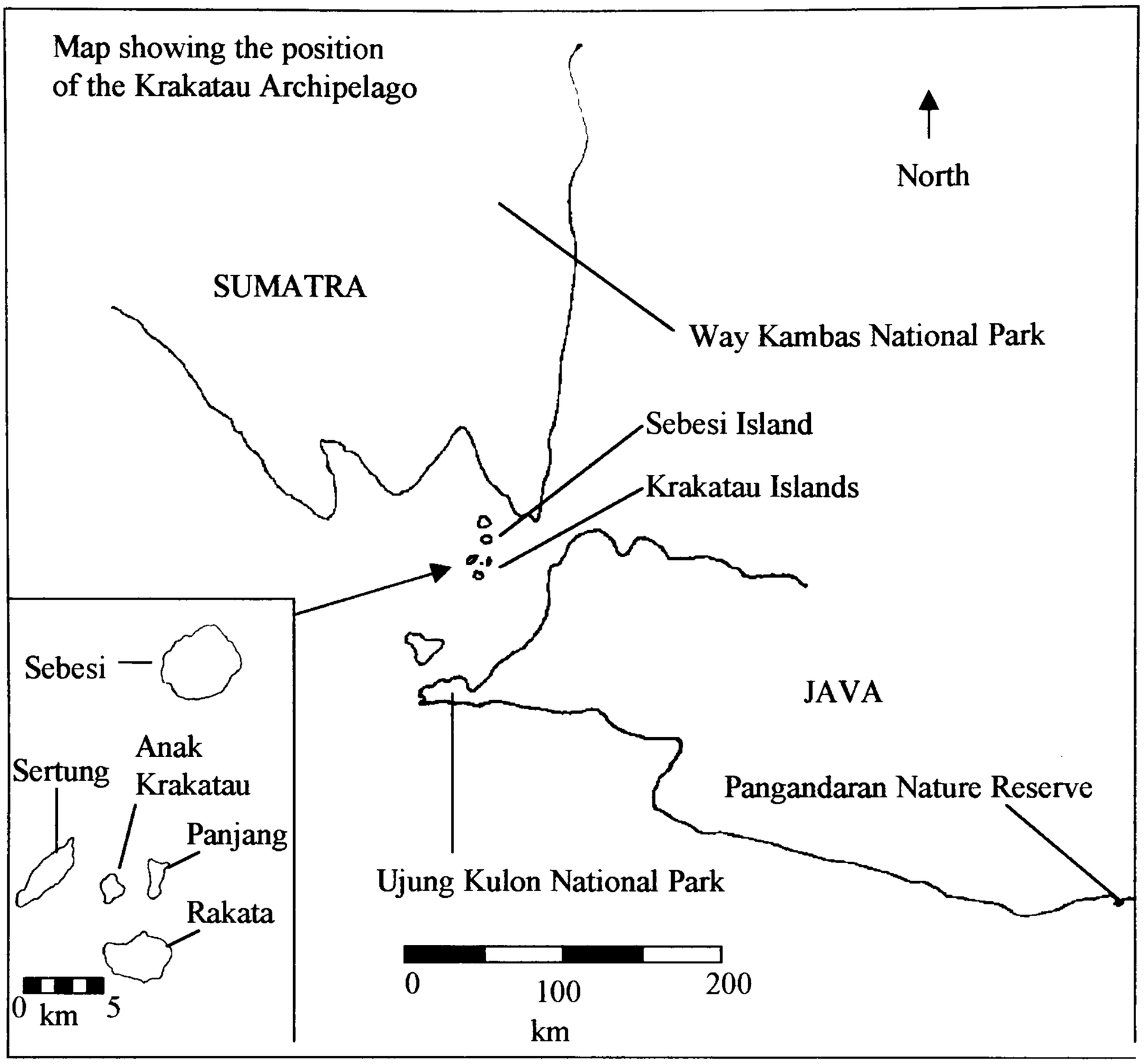
Figure 1.1
Map of Sundaland, showing the principal
places mentioned in the text.
Shaded areas are
mountains over 500m a.s.l.

It has been proposed that the huge lava flows are the cause of one of Sumatra's biogeographic boundaries, that the tuffs acted (and act) as a dispersal barrier to plants and animals (Whitten *et al.* 1984, Laumonier 1997). However, it is unlikely that the putative effect of these tuffs will have affected the distributions of most of the biota, for they were probably dispersed long before 74 Ka.

Probably the most famous volcanic eruption in the region was that of Krakatau. On 27 August 1883 more than half of the island of Krakatau was destroyed in a series of devastating eruptions. The remaining part of the island (now called Rakata) and the other two islands in the group (Panjang and Sertung) were covered by up to 60 m of very hot volcanic ejecta (Dammerman 1922,1948, Thornton 1996). The human cost of the eruption was great; over 30,000 people were killed by either eruption-induced tsunamis or the fall of hot ash and debris (Dammerman 1922, Thornton 1996).

It is probable that all animal life on the Krakatau islands was killed by the eruption (Dammerman 1922). If any plant stocks survived, they are thought to have been so rare that their effect on later studies of colonisation and establishment would be negligible (Dammerman 1922, Thornton 1996, Whittaker *et al.* 1999). This biological "clean slate" has allowed researchers an almost unique opportunity to study the processes of island colonisation and to test biogeographical theories (Thornton 1996).

After the eruption, life rapidly returned to the islands. In 1886, three years after the eruption, between 24 and 26 species of vascular plant were found on Rakata (Thornton 1996) and by 1908, 196 animal species were found (Dammerman 1922). Now more than a century after the eruption, the islands are fully forested (Bush *et al.* 1995, Whittaker *et al.* 1999) and support a large and varied fauna (Thornton & New 1988, Winoto Suatmadji *et al.* 1988, Rawlinson *et al.* 1990, Zann *et al.* 1990, Thornton 1996).



Vegetation

Most of Sundaland's natural vegetation is rainforest. This grows in areas where there is usually over 2,000 mm rainfall p.a. and there is little or no seasonal drought (Cranbrook & Edwards 1994). The forest tends to be tall and evergreen. A few areas are more seasonal, particularly north Java and Madura. In these areas the vegetation is mainly deciduous and in the north east of Java there is even savannah vegetation (Whitten *et al.* 1996, van Assen 1993).

The rainforests are a dynamic ecosystem and it is thought that they were considerably affected by Quaternary glaciations (Kaars & Dam, 1995; Morley, 2000). During glaciations most of the vegetation was probably a mixture of

forest (Morley, 2000). Obligate rainforest species are likely to have been confined to a few refugia in northern Borneo, northern Sumatra and the Mentawai islands (Brandon-Jones, 1998). During interglacials rainforest recolonised the region (Kaars & Dam, 1995; Morley, 2000).

Figure 1.3 Lowland mixed dipterocarp rainforest on Sungai Busang, Central Kalimantan, Indonesia

Humans and human disturbance

The earliest evidence of humans in the region is Java man, *Homo erectus*, who is thought to have been in the region since the Plio-Pleistocene (Whitten *et al.* 1996), though the dating is controversial. *Homo sapiens* arrived in the region

by about 40,000 years before present (BP, in corrected years), if not earlier (Cranbrook 2000). There are indications of rice found in Sulawesi as early as about 6000 BP (Whitten *et al.* 1996), and it is thought that these early farmers practised swidden agriculture in a similar manner to today (Cranbrook 2000). In Java, where the climate is more seasonal, teak was introduced by the Hindus in about 200-400 AD, which rapidly spread to cover about 1.5 million Ha by 1000 AD (Whitten *et al.* 1996). The fertile volcanic soils of Java also allowed much wet rice (*sawah*) cultivation. Under the Dutch there was much deforestation and by the turn of the 20th century, most of the forest had gone (Whitten *et al.* 1996). Thailand has also lost much of its natural rainforest, due to logging and changing land use due to a great increase in population (Stewart-Cox 1995). Peninsula Malaysia too was largely untouched until this century, though now most of the natural primary forest has gone, to be replaced by agriculture, rubber, oil-palm and logged forest. Borneo and Sumatra were less disturbed until after the second world war, when commercial interests in timber, rubber and palm oil, as well as a rise in the population has led to much of the land use being changed and much loss of primary rainforest (MacKinnon *et al.* 1997). Now there is grave concern about the future of the rainforest of the Sunda region (Jepson *et al.* 2001), with many species, and in fact the whole primary lowland rainforest ecosystem facing extinction (van Schaik *et al.* 2001, Jepson *et al.* 2001).

Termites

Worldwide, there are over 2600 species of termite in 281 genera (Kambhampati & Eggleton 2000).They can be divided into seven families, the Termopsidae, Serritermitidae, Hodotermitidae, Kalotermitidae, Mastotermitidae,

Rhinotermitidae and the Termitidae. The first six families are known as the lower termites, while the Termitidae (which make up more than 75% of the species found worldwide) are known as the higher termites (Collins 1989). Only three families are found in Sundaland: the Kalotermitidae, Rhinotermitidae and the Termitidae (Tho 1992).

Termites are thought to have arisen in the Jurassic, before the breakup of Pangaea (Eggleton 2000). Their evolutionary history is only now being systematically investigated, and it appears that their diversification has followed the presence of large megathermal forest blocks (Davies 2001). Sundaland is relatively poor in termite species richness and biomass when compared to the Afrotropics and the Neotropics (Eggleton *et al.* 1999). This is thought to be a result of Sundaland's isolation from the main centres of speciation in Gondwanic South America and Africa and the lack of a long-lasting (in terms of tens of millions of years) large rainforest block (Davies 2001).

Termites are eusocial insects, found on every continent except Antarctica. They are divided into several castes: soldiers, workers, alates (winged reproductives) and the (wingless) reproductive king and queen. The king and queen (or sometimes several kings and queens) are fed and cared for by the sterile workers. These also care for the eggs and immature nymphs, build the nest (or hollow it out if it is in wood), forage for food (either building foraging tunnels overground, excavating tunnels in the soil or foraging freely above the ground) and feed and care for the soldiers. The soldiers are adapted to defend the colony, by either using their mandibles to slash or cut predators or, in the case of the subfamily Nasutitermitinae by having a protruding fontanelle, which squirts poisonous secretions at attackers (Collins 1989). Alates are the only winged caste,

and are the reproductives of the colony. The alates fly about once a year (generally at the onset of the rainy season), and if not killed (alate mortality is generally estimated to be about 99.9%) they find a mate, shed their wings and find a suitable nesting site. This site is generally close to the parent colony, for alates generally only fly a few metres (Nutting1969).

Termites are detritivores, feeding on wood, grass, bryophytes, living trees, leaf litter and soil, in various states of decay (humification). These different food sources represent a humification gradient (with soil being at the highly humified end, and living plant material at the highly un-humified end). Four feeding groups have been erected which incorporate both the termites' phylogenetic position and the position of their food source on the humification gradient. They are placed into one of four feeding groups according to worker morphological characters (shape of pronotum, mandible and enteric valve characters (Donovan *et al.* 2001a)). The feeding groups are numbered sequentially as their principal food source becomes more humified: I: Wood, litter and grass feeders (all lower termites), II: Wood, litter and grass feeders (some of the higher termites), III: Very decayed wood or high organic content soil and IV: Low organic content soil. A full list of termite genera and their feeding group assignations can be found in Donovan *et al.* (2001a).

Termites use a variety of microorganisms in the gut to break down their food into a more digestible form. The guts of the lower termites contain Archaea, bacteria and Protozoa, while only Archaea and bacteria are found in the Termitidae (Brauman *et al.* 2001).

Sundan termites can also be placed into one of nine functional taxonomic groups (FTGs), following Davies (2001). These represent a combination of the

taxonomic and functional position of the termite. In some cases a FTG can be a whole family or subfamily, in other cases they are simply a group within a subfamily. These different feeding group and FTG classifications have been found to be very useful when analysing patterns of termite diversity on a regional or global scale (Davies 2001).

Table 1.1 Showing the different termite functional taxonomic groups found in Sundaland; their nesting sites and their food sources.

Family/subfamily and FTG	No. described spp. In region	Nesting sites	Feeding group	Food source
Kalotermitidae	34	Hard dead wood	I	Hard dead wood
Rhinotermitidae	21	Hard to soft dead or live wood	I	Hard to soft dead or live wood
Termididae: Macrotermitinae	30	Epigeal mounds	II	Dead wood or litter
Terminae: Amitermes group	20	In soil, epigeal mounds, arboreal nests or in wood	II	Living or dead wood or humified soil.
Foraminitermes group	3	In soil or epigeal mounds	III	Soil
Termes-Capritermes group	38	In soil or epigeal mounds, rarely in dead wood	III and IV	Soil, humified soil or very decayed wood.
Apicotermitinae	1	In soil	III	Humified soil
Nasutitermitinae Wood feeding group and soil feeding group	72	In soil, wood or arboreal nests	II or III	Epiphytes, live or dead wood or humified soil

1.2 Sundan termite research: A review.

Ecological work

Though the termites of the Sunda region have been studied and described since 1858 (Hagen 1858), until the 1970s most work on termites was related to their pest status and their control (Tho 1992).

In the 1970s ecological work began on termites, emphasising their importance in the rainforest ecosystem (Collins 1989). Abe and Matsumoto studied many aspects of termite ecology in Pasoh Forest Reserve, West Malaysia, including assemblage composition (Abe 1978a), distribution (Abe & Matsumoto 1978), the role of termites in the breakdown of dead wood on the forest floor (Abe 1978b), food and feeding habits (Abe 1979), and abundance (Abe & Matsumoto 1979). Abe and Matsumoto made the first estimate of termite population density in Sundan rainforest (*c.* 3500 m^{-1}), showed the importance of subterranean termites (which had been largely ignored, as they are hidden and small), and demonstrated that termites are an extremely important part of the soil macroinvertibrate fauna. They were also the first to estimate litter and wood consumption by termites in the region; a total of 155-173 g m^{-2} yr^{-1} (Abe & Matsumoto 1979).

Abe's (1984) survey of Krakatau, Panaitan island and Java led him to propose that termites colonise islands by rafting, rather than flight, which has had a great impact on the study of termite biogeography.

Tho (1982) also did valuable work on termite ecology, discovering that the ring-barking of trees by *Microcerotermes dubius* can play a key part in forest gap

ɔrtant parts of the basic natural history and ecology of *Dicuspiditermes nemorosus* and *Cryptotermes cynocephalus*.

Figure 1.4 Nest of *Dicuspiditermes nemorosus*.

Some of the most important ecological work on termites was carried out by Collins, on the 1978-9 Mulu expedition. He compared the termites of three different natural forest types: Mixed dipterocarp, kerangas and alluvial forest, and showed that alluvial forest has a very different composition to the other two types, due to frequent flooding (Collins 1979). He also demonstrated the importance of

termites in decomposition processes (Collins 1983, 1989). Collins was the first researcher to investigate the effects of forest clearance on termites, showing that it affects different subfamilies in different ways (Collins & Furtado 1980). Perhaps his most important ecological work was his study of the effects of altitude on soil macrofauna (Collins 1980), where he showed that termite biomass significantly declines with increasing altitude.

In most of the work so far described, the sampling methods were labour intensive and were not standardised, so work by different authors in different areas cannot be compared directly. Members of the Termite Research Group, Natural History Museum, London, therefore developed a standardised sampling protocol. Jones and Eggleton (2000) have demonstrated that the method gives a representative sample of both the taxonomic composition and the functional group composition of the local termite assemblage.

This protocol was first used in Pasoh Forest Reserve (Jones & Brendell 1998). With this protocol, termite researchers have been able directly to compare different sites and have been able to come to a far better understanding of termite ecology, evolution and biogeography.

The transects have chiefly been used in Sundaland to investigate the effects of different levels of disturbance, in Danum Valley Conservation Area in Sabah (Eggleton *et al.* 1997, 1999), a forestry concession in Tabalong district, South Kalimantan (Jones & Prasetyo in press) and across a disturbance gradient in Jambi province, Sumatra (Jones *et al.* unpublished data). These studies have found that logging and other land use changes have a significant effect on termite species composition, richness and abundance. Logged forest tends to have fewer

species, a lower abundance and a greater proportion of wood feeders (groups I and II) than primary forest.

The transect method was also used to investigate the recolonisation of the Krakatau islands by termites, to test Abe's (1984) hypothesis that only rafting termites are able to colonise islands. In 1996, Gathorne-Hardy *et al.* (2000) surveyed the termites from Java, Sumatra and the Krakatau islands, using the standardised sampling protocol. Previous surveys of the Krakatau islands and their probable source areas had not been sampled in a systematic manner (Holmgren 1913-14, Dammerman 1922, 1948, John 1925, Kemner 1934, Roonwal & Maiti 1966, Roonwal 1969, Amir 1975, Abe 1984) so direct comparisons of the assemblages of different sites had not been possible. Gathorne-Hardy *et al.* (2000) found that no soil nesting species of termite is present on the Krakatau islands, though they are common on the mainland (63% of the termites found on the mainland in this study were soil nesting species), and make up six out of the 13 species found on Sebesi island.

All of the termite species found in the archipelago nest in wood (for at least some stage of the life of the colony) and therefore all have the ability to colonise by rafting from the mainland. That no soil-nesting termite is found on the Krakatau islands, and that all species present on the islands are able to raft led Gathorne-Hardy *et al.* (2000) to support Abe's (1984) hypothesis that termites have colonised the Krakatau islands by rafting only.

The transect method has also been used to compare the termite assemblages of Sundaland with those of other regions. This has led to an increased understanding of the evolution of the order and of the different functional taxonomic groups (Davies 2001).

Taxonomy forms the foundation on which other all aspects of biology rest (Eggleton 1999), and as such the study of the termites of Sundaland are on comparatively firm foundations (Eggleton 2000).

The taxonomy of the Sundan termites has been studied for more than a century. The first major work on the termites of Sundaland was Haviland's Observation on Termites (1898), in which he described 56 new species from the region. This work is still valuable today and his illustrations have been reproduced for recent taxonomic works (e.g. Krishna, 2001). Other taxonomists, such as Holmgren (1912-14) and Kemner (1934) also worked in the region and made significant taxonomic advances. After the war, Emerson (1960), Krishna (1968, 1972, 2001), Ahmad (1958, 1965, 1968), Ahmad & Akhtar (1981), Roonwal & Maiti (1966), Thakur & Thakur (1992), Tho (1992) and Thapa (1981) have all made major changes and additions to the systematics of Sundan termites.

The most valuable taxonomic work is the revisionary monograph, where species are not only described but where redundant names are also synonomised (Eggleton 1999). In recent works on Sundan termite taxonomy there have been very few synonomies. Three of the most influential modern works (Ahmad 1968, Ahmad & Akhtar 1981 and Thapa 1981), which between them erected ten genera and 47 species, have only one synonomy. Tho's (1992) work is much more rounded, with many synonomies, but was unfortunately unfinished.

1.3 Fieldwork and taxonomic methods.

In all of the fieldwork that I undertook, I collected termites using the standardised transect method (Jones & Eggleton 2000), as follows:

[redacted]cts, 100 m long by 2 m wide at random through the forest, incorporating habitat heterogeneity. Each transect is divided into 20 sections, each 5 m long, and in each section spent one man-hour searching for termites. Within each section the following microhabitats I examined for termites: (i) A dozen areas of surface soil of about 12 cm x 12 cm and 10 cm deep with associated leaf litter were scraped up and examined for termites. (ii) Dead wood with a diameter of < 0.5 cm is broken open and termites were removed. (iii) Tree trunks and buttress roots were examined. Particular attention was paid to the deep accumulations of litter and organic-rich soil between buttresses and to the soil in and below very rotten logs. Any carton sheeting or runways were scraped off and examined, up to a height of 2 m. (iv) Termite nests were opened and termites collected.

Figure 1.5 Searching for termites: digging soil scrapes.

worker castes were collected (if they were present) and stored in 90% ethanol. Alates were excluded because their presence does not necessarily imply the presence of a viable colony within the transect.

Figure 1.6 Collecting termites: putting specimens into a tube of alcohol

I identified all of the termites that I collected at the Natural History Museum (BMNH), London. They have been deposited at the Bogor Zoology Museum, Indonesia with duplicates at Syiah Kuala University, Banda Aceh, Indonesia and at the BMNH. Specimens were identified to species or, where this proved impossible, to numbered species. These were numbered in accordance with Tho (1992), material from Danum Valley Conservation Area (Eggleton et al. 1997, 1999) and the Maliau Basin in Sabah (Jones et al. 1998, Jones 2000), Jambi (Jones, unpubl. data) and from Pasoh Forest Reserve in Peninsular Malaysia (Jones and Brendell 1998).

1.4 Content

In order to understand the biogeography of the Sundan termites, much basic ecological, taxonomic and survey work was necessary, and many simple questions needed to be answered before more complex hypotheses could be proposed and tested.

Each of the chapters stands alone and each had its own, specific aims that work towards the overall project aims. Chapters two, three and four are baseline studies, while chapters four and five build on the results of this work. In chapter two I investigated the termite composition of Sulawesi, comparing it to Borneo and Sumatra and illustrating the colonising abilities of different termite groups over geological and evolutionary time scales.

Chapter three found the response of termites to changes in altitude and rainfall, from data generated from a survey of the Leuser Ecosystem. Chapter four is a taxonomic chapter, showing some of the taxonomic problems encountered and the changes made to overcome them.

With the understanding of termite dispersal patterns and taxonomy gained in chapters two to four, it was possible for me to hypothesise that termites would be able to act as indicators of Quaternary climate change in Southeast Asia. The fifth chapter investigated the extent of Quaternary climate change and discusses a possible complete history of the region.

In chapter 6, using all data collected so far, I investigated the effects of different types of disturbance on the termite functional taxonomic group composition as well as discussing the rate at which termites recolonise disturbed areas and the implications of these patterns.

Chapter 7 is a synthesis, pulling together some of my findings in this project and suggesting further work.

CHAPTER TWO

ISLAND COLONISATION

A version of this chapter has been published as: Gathorne-Hardy, F. J, Collins, N.M., Buxton, R.D. and Eggleton, P. **2000**. A faunistic review of the termites (Insecta: Isoptera) of Sulawesi, including an updated checklist of the species. *Malayan Nature Journal.* 54: 347-353.

2.1 Introduction

The termite fauna of the Krakatau archipelago is markedly different to that of the mainland, having only wood-nesting species (Gathorne-Hardy *et al.* 2000, chapter 1). This is probably to be expected, for there has been little more than a century for the termites to reach the islands and establish colonies. It may be that termites, given a longer time, can cross water gaps by flight and establish colonies. To properly investigate termite colonisation of islands, over an evolutionary timescale, a far older island site is needed.

In the accessions drawers of the termite collections of The Natural History Museum, I found a collection of unidentified termite material from Sulawesi. This had been collected from the Dumoga-Bone and Tangkoko National Parks in North Sulawesi by R. D. Buxton and N.M. Collins in 1985, as part of the Royal Entomological Society's Project Wallace. From their collection notes, I could see that they had effectively sampled the termites of their study site, so it was clear that this collection could help to answer questions about the long-term colonisation abilities of termites.

Sulawesi (Celebes), the most westerly island in Wallacea (Dickerson *et al.* 1928) has been an island for at least 45 million years (Moss & Wilson 1998). It is only about 100 km from the mainland (Borneo is part of the Sunda shelf and has been joined to the mainland for at least the past 30 million years (Hall 1998)). Sulawesi has a complex geological history. In the mid-Eocene (about 45 million years ago) the northern, western and southern arms broke away from Borneo and formed the Makassar straits (Moss & Wilson, 1998), which to this day separate Sulawesi from the Sunda shelf. From the Oligocene until the mid-Miocene much of Sulawesi was submarine, though it is thought that volcanic islands may have remained emergent (Moss & Wilson, *op. cit.*). The eastern arm of Sulawesi (part of the Australian plate) drifted westwards under water through the Eocene and Oligocene and joined the rest of Sulawesi in the early Miocene. By the Pliocene, Sulawesi's coastline was similar to that of today (Moss &Wilson, *op. cit.*).

The island of Sulawesi (area 18,904 ha), is dominated by hills and mountains (83% of the island has been classified as "hilly to mountain" land) and 20% of the land area is above 1000m a.s.l. (Whitten *et al.* 1987). Most of Sulawesi is permanently humid and, until recently, was forested (Whitten *et al.* 1987). This island has been of great interest to biologists, having a large number of endemic species (62% of the mammals-including bats-are endemic (Whitten *et al.* 1987)) and being the westernmost to which the Australian mammals and birds penetrate into Asia (Wallace 1880, 1911).

During the Quaternary, glaciation-induced climate change caused widespread forest fragmentation in Southeast Asia (chapter 5). Though sea level has changed considerably in the past two million years (Haq *et al.* 1987), the sea bed around Sulawesi is sufficiently low that its land area hardly changed, even when the sea level

was at its minimum of 120 m below that at present (Voris 2000). The fact that Sulawesi was still an island, and its topography of being mountainous with a long coastline, probably buffered it from the worst effects of this climate change.

Figure 2.1

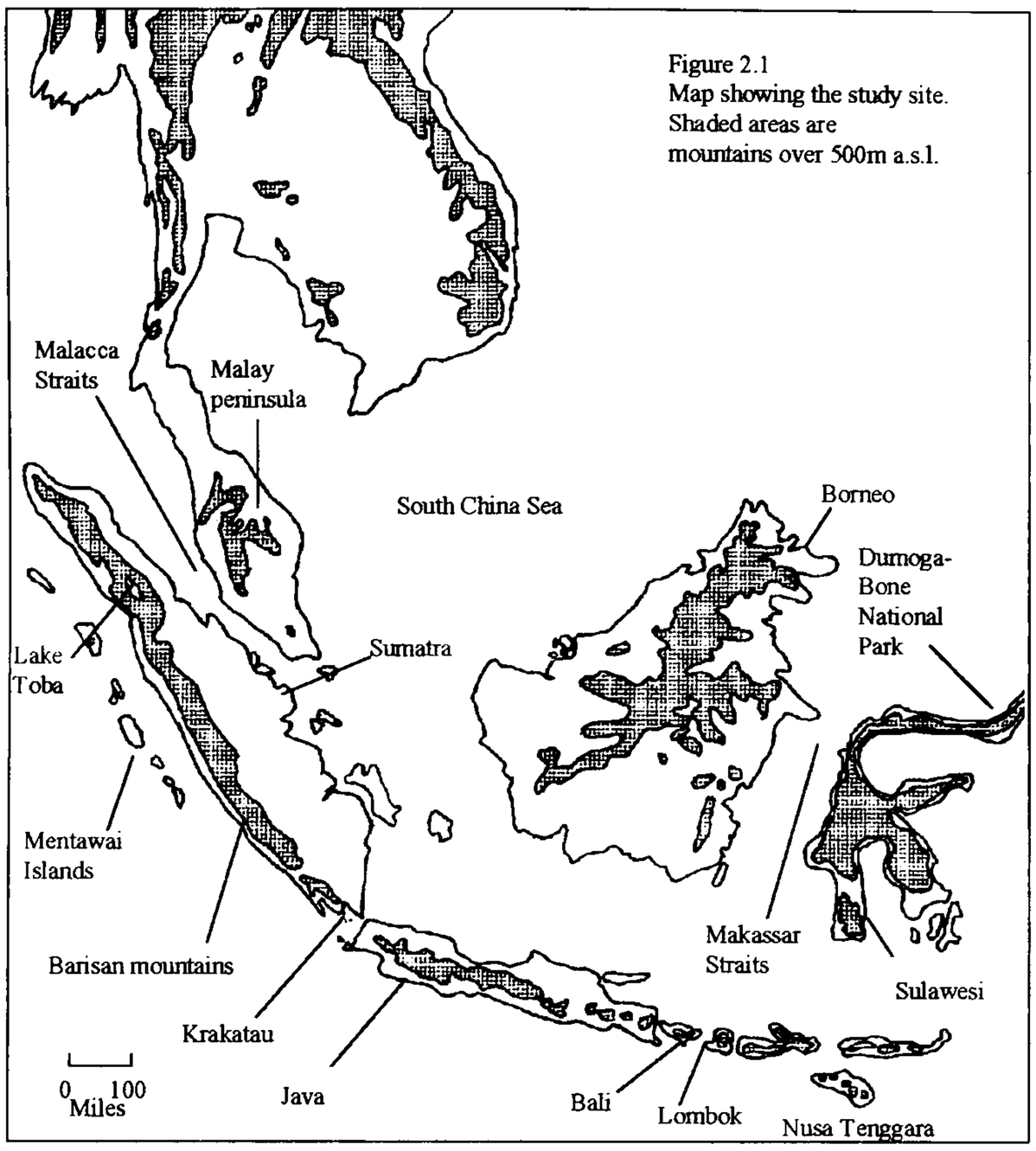


Figure 2.1
Map showing the study site. Shaded areas are mountains over 500m a.s.l.

2.2 Methods

Collecting methods

Collins (who had had much previous experience at collecting termites from all microhabitats) and Buxton thoroughly searched through ten 10 x 10 m plots, searching in the microhabitats where termites are usually found. Any termites discovered were collected. Outside these plots, large pieces of dead wood were

opened and the termites collected when they were encountered. Living trees were examined to see if they had been "piped" by *Coptotermes*.

Termites of both worker and soldier castes were collected and stored in 80% ethanol. This is the first published collection of Sulawesi termites since Kemner's in 1934.

Identification

I identified the termites collected to either named or numbered species at the Natural History Museum (BMNH), London.

2.3 Results

In the Sulawesi collection were 22 species of termite in 15 genera (these are shown in Table 1, along with all of the other species ever found on the island). Of the species found in this study, nine are new to science. One of these has since been described (see chapter 4, Gathorne-Hardy 2001). Eight genera (*Cryptotermes, Parrhinotermes, Prorhinotermes, Pericapritermes, Diwaitermes, Hirtitermes, Lacessititermes* and *Hospitalitermes*) have not been collected from Sulawesi before. Only one species of termite that is known to be an obligate soil-nester (*Odontotermes boetonensis*) was found.

No true soil feeder (group IV) was found and only one species (*Pericapritermes* sp. nov. 1) of group III feeders was found (the feeding groups are explained fully in Chapter 1).

Table 2.1. Showing a complete checklist of the termites of Sulawesi. The collectors are shown.

			Nest site	Feeding group	Collector/Author
KALOTERMITIDAE					
Cryptotermes	*cynocephalus*	Light	Wood	I	RDB & NMC, 1985
Cryptotermes	*domesticus*	(Haviland)	Wood	I	RDB & NMC, 1985
Glyptotermes	*sepilokensis*	Thapa	Wood	I	RDB & NMC, 1985
Glyptotermes	*brevicaudatus*	(Haviland)	Wood	I	RDB & NMC, 1985
Glyptotermes	sp. nov. 1		Wood	I	RDB & NMC, 1985
Neotermes	*tectonae*	(Dammerman)	Wood	I	RDB & NMC, 1985
Neotermes	*saleierensis*	Kemner	Wood	I	Kemner, 1934[1]
Neotermes	*ketelensis*	Kemner	Wood	I	Kemner, 1934
Kalotermes	*indicus*	Holmgren	Wood	I	Kemner, 1934
RHINOTERMITIDAE					
Coptotermes	*curvignathus*	Holmgren	Wood	I	RDB & NMC, 1985
Coptotermes	*menadoensis*	Oshima	Wood	I	Kemner, 1934
Coptotermes	*minutissimus*	Kemner	Wood	I	Kemner, 1934
Coptotermes	*pergrinator*	Kemner	Wood	I	Kemner, 1934
Coptotermes	*boetonensis*	Kemner	Wood	I	Kemner, 1934
Heterotermes	*pamatatensis*	Kemner	Wood	I	Kemner, 1934
Parrhinotermes	sp. nov. 1		Wood	I	RDB & NMC, 1985
Prorhinotermes	*flavus*	Bugnion & Popoff	Wood	I	RDB & NMC, 1985
Schedorhinotermes	*brevialatus*	(Haviland)	Wood	I	RDB & NMC, 1985
Schedorhinotermes	*medioobscurus*	(Holmgren)	Wood	I	RDB & NMC, 1985
Schedorhinotermes	*makassarensis*	Kemner	Wood	I	Kemner, 1934
Schedorhinotermes	*celebensis*	(Holmgren)	Wood	I	Kemner, 1934
TERMITIDAE					
Termitinae					
Microcerotermes	*distans*	(Haviland)	Wood/Arboreal	II	RDB & NMC, 1985
Microcerotermes	*celebensis*	Kemner	Wood/Arboreal	II	Kemner, 1934
Pericapritermes	sp. nov. 1		Wood/Soil	III	RDB & NMC, 1985
Macrotermitinae					
Macrotermes	*gilvus*	Hagen	Soil	II	Holmgren, 1913[2]
Odontotermes	*boetonensis*	Kemner	Soil	II	Kemner, 1934, RDB & NMC, 1985
Odontotermes	*menadoensis*	Kemner	Soil	II	Kemner, 1934
Odontotermes	*celebensis*	Kemner	Soil	II	Kemner, 1934
Odontotermes	*makassarensis*	Kemner	Soil	II	Kemner, 1934
Odontotermes	*djampensis*	Kemner	Soil	II	Kemner, 1934
Nasutitermitinae					
Bulbitermes	sp. nov. 4		Wood/Arboreal	II	RDB & NMC, 1985
Bulbitermes	sp. nov. 6		Wood/Arboreal	II	RDB & NMC, 1985
Bulbitermes	sp. nov. 7		Wood/Arboreal	II	RDB & NMC, 1985
Diwaitermes	sp. nov. 1		Wood	II	RDB & NMC, 1985
Hirtitiermes	*brabazoni*	Gathorne-Hardy	Wood	II	RDB & NMC, 1985
Hospitalitermes	*rufus*	(Haviland)	Wood/Soil	II	RDB & NMC, 1985
Lacessititermes	sp. nov. 1		Wood/Arboreal	II	RDB & NMC, 1985
Nasutitermes	*matangensis*	(Haviland)	Wood/Arboreal	II	RDB & NMC, 1985
Nasutitermes	*celebensis*	(Holmgren)	Wood/Arboreal	II	Kemner, 1934
Nasutitermes	*makassarensis*	(Kemner)	Wood/Arboreal	II	Kemner, 1934
Nasutitermes	*salierensis*	(Kemner)	Wood/Arboreal	II	Kemner, 1934
Nasutitermes	*boengeinsis*	(Kemner)	Wood/Arboreal	II	Kemner, 1934

[1] I have not been able to examine Kemner's material. In the light of the large amount of termite taxonomy published since 1934 it is possible that not all of his species are valid.

[2] Kemner (1934, p 25) convincingly argues that Holmgren's (1913) record of *M. gilvus* from Sulawesi is mistaken and that it is not found east of Wallace's line.

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2.4 Discussion and conclusions

Of the termites so far recorded from Sulawesi, no termite genus is endemic. At species level, all Sulawesi *Odontotermes* are endemic (*Odontotermes* builds very obvious nests and some species are pests, so its distribution is well known) and presumably so are many of the new species discovered in this study. However, the termites of South East Asia have been incompletely surveyed, so some level of pseudo-endemism is likely.

All of the termite genera found on Sulawesi are efficient colonisers (Abe, 1984) and widely dispersed; either within the region or globally (Eggleton, 2000; Tho, 1992; Roisin & Pasteels, 1996; Gathorne-Hardy *et al.* 2000). Termite alates (winged reproductives) tend to be poor fliers (Sen-Sarma, 1968; Nutting, 1969; Abe, 1984), so it is thought that the majority of termites colonise islands only by rafting in dead wood (Abe, 1984). Only those species which nest in wood are able to raft (Abe, 1984).

Most of the Sulawesi genera (except *Odontotermes* and *Pericapritermes*) have already been identified as rafting or potentially rafting termites and are often pre-adapted for this method of dispersal (Abe, 1984; Gathorne-Hardy *et al.* 2000).

Pericapritermes is known as a soil-nesting termite (Abe, 1984; Eggleton *et al* 1997). However, it has been seen nesting in dead wood (nymphs and alates found in dead wood in Borneo; personal observations) so it is quite possible that the ancestors of *Pericapritermes* sp. nov. 1 rafted across the 100 km Makassar straits from Borneo.

Although the Macrotermitinae are obligate soil-nesters (which prevents *Odontotermes* from having colonised Sulawesi by rafting), they are thought to have crossed the 300 km Mozambique channel from Africa to Madagascar by flight

(Emerson, 1955, Eggleton & Davies in press). It is possible therefore, that the Sulawesi *Odontotermes* species could have flown across the 100 km Makassar straits.

The three *Odontotermes* species present on Sulawesi are all very similar, sharing many taxonomic characters. In particular they have a similar soldier head size and position of the marginal tooth on the left mandible (Kemner, 1934). These characters vary considerably among the several species of *Odontotermes* on the Sunda shelf and are taxonomically important (Kemner, 1934, Thapa, 1981, Tho, 1992). The homogeneity of the Sulawesi species (taken in conjunction with the wide morphological variation in the Sundan *Odontotermes* species) suggest that the three Sulawesi *Odontotermes* species are closely related and may be descended from a single colonising ancestor.

Termites have been present on Sulawesi long enough for endemic species to evolve (i.e. the three *Odontotermes* species). Functionally however, all of the present fauna are the same as their con-generic relations on the Sunda shelf. It appears that no great adaptive radiation event has taken place; that termites have not filled unoccupied ecological niches.

Of soil feeding termites (feeding groups III and IV), only *Pericapritermes* sp. nov. 1 has been recorded from Sulawesi. Termites of feeding groups III and IV make up 44% of the termite species richness in lowland rainforest in northern Sumatra (Chapter 3), 37% in Pasoh Forest Reserve in Peninsular Malaysia (Jones & Brendell, 1998) and 58% of the termite species richness of Sabah in Borneo (Eggleton *et al.* 1997).The Sulawesi termite assemblage is therefore functionally depauperate when compared with the Sunda shelf assemblages. Earthworms too are found in much lower numbers than in Borneo. In litter samples only three earthworms were found in $24m^2$ litter (Hammond, 1990) compared with $>35m^{-2}$ (below the altitude of 1650m)

on Gunung Mulu in Borneo (Collins, 1980). The rarity of these soil macroinvertibrates, which are both important ecosystem engineers (Anderson, 1995) will probably have affected many of the soil properties of Sulawesi.

On Sulawesi only those termites which are capable of crossing a sea barrier are present. For termites therefore, as with vertebrates (Cranbrook, 1981, Musser, 1987), Sulawesi should be considered an oceanic island (it has a termite assemblage typical of oceanic islands, such as Mauritius (Moutia, 1936) and the Solomon Islands (Harris, 1957)), with a fauna derived from the dispersive elements of both the Sundan and Australian biogeographical regions. Though it is thought that volcanic islands remained emergent during the Oligocene (Moss & Wilson, 1998), any eruptions on them would have had a devastating effect, similar to that of Krakatau (Thornton, 1996). It is therefore unlikely that the emergent volcanic parts of Sulawesi could have acted as "Noah's arks" (Audley-Charles, 1987) or long-term refugia of Eocene or pre-Eocene Asian flora and fauna.

THE LEUSER ECOSYSTEM

A version of this chapter has been published as: Gathorne-Hardy, FJ, Syaukani and Eggleton, P. **2001**. A baseline survey of the termites (Isoptera: Insecta) of the Leuser Ecosystem (Sumatra, Indonesia). *Journal of Tropical Ecology* 17: 379-393.

3.1 Introduction

A prerequisite to understanding the biogeography of the termites of Sundaland is to understand their ecology at a regional scale, across relevant environmental gradients. The Leuser Ecosystem is an area very suitable for such work

The Leuser Ecosystem (LE) is a large area (2.5 million ha) of land in northern Sumatra, Indonesia. The Gunung Leuser National Park (GLNP) lies within its boundaries. The LE is managed by the Leuser Development Programme (LDP), a joint Indonesian and EU supported non-governmental organisation designed to integrate local development and conservation.

A large proportion of the LE - most of the GLNP and much of the land to the north - is still primary rainforest. The LE has a wide range of forest types, from swamp forests, through lowland dipterocarp forest up to high altitude sub-alpine vegetation (de Wilde & Duyfjes 1996). It is thought to be a Quaternary refugium (Brandon-Jones 1998) and is one of the last areas in the world where elephants, tigers, rhinoceros, orang utan and clouded leopards all occur in the same ecosystem. The flora of the LE

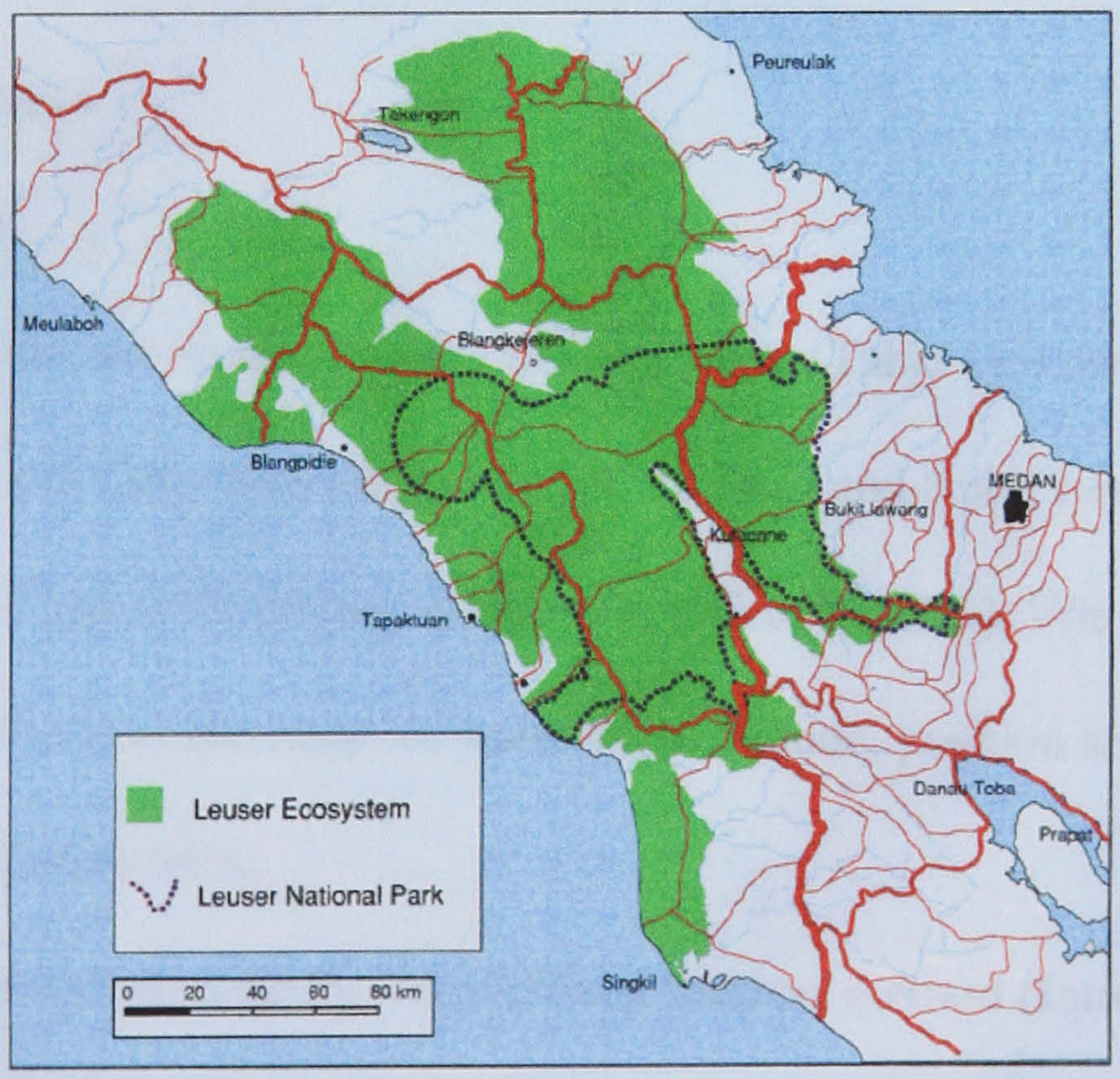
is very rich, with the highest number of species of *Rafflesia* found in any one area (Meijer 1996) and a high rate of plant endemism (de Wilde & Duyfjes 1996). MacKinnon & MacKinnon (1986) considered the GNLP to be the most important of all conservation areas in the Indomalayan region.

Topologically the LE is composed of two mountain ranges (the West Barisan and West Alas mountains to the west and the East Barisan mountains to the east) divided by a central rift valley (the Alas Valley), with plains to the east and west of the mountains (van Beek 1996).

Undisturbed lowland rainforest is unfortunately comparatively rare in the LE, mainly due to logging or conversion to crops or oil-palm cultivation. The remaining lowland forest is severely threatened, particularly in the present economic crisis (van Schaik *et al.* 2001).

Figure 3.1

Leuser Ecosystem and National Park



Although the more inaccessible mid-altitude forest (at about 1000 m) is relatively common in its pristine state, it too is under increasing threat.

Here I present a baseline survey of the termites of the LE. This is the first time that the termites of such a large area of continuous rainforest have been surveyed using strictly standardised methods. In this survey I have assessed variation in composition, species richness and abundance in the termite assemblages over altitudinal and geographical gradients.

This baseline is intended to be the first of a series of studies in the LE. Termites have never been studied over such a large area for a long period of time. Syaukani (of Syiah Kuala University) is in the process of investigating the Leuser termites over time, re-surveying the sites covered in this chapter and assessing the impacts of any change to the forest. In three sites the forest has been cleared for agriculture since it was first surveyed. Undisturbed primary sites have also been re-surveyed to provide an indication of how the termite fauna changes over time.

3.2 Methods

Sampling

I ran one or more transects at each site (Table 1). I also sampled termite abundance at three sites (Ketambe 500 m, Suaq and Bukit Lawang 250 m). Definitions of lowland and sub-montane forest follow Grubb (1971). The choice of study sites was intended to cover the range of variation in altitude, position and potential disturbance within the Ecosystem.

I sampled using the standardised transect method (Introduction, Jones & Eggleton 2000). Termites were also casually collected at each site.

Table 3.1. Positions and altitudes of sites from which termites were sampled in the Leuser Ecosystem, Sumatra, Indonesia, with forest type. [P] indicates protected forest.

Site	Position		Altitude (m)	Forest type
	N	E		
Suaq Belimbing field station	03° 03' 29"	97° 26' 41"	125	Primary lowland dipterocarp rainforest. [P]
MRT Logging concession	03° 11' 41"	97° 24' 4"	200	Primary lowland dipterocarp rainforest. Logged in 1999
Krueng Baru	03° 38' 57"	97° 00' 22"	200	Highly disturbed lowland rainforest.[1]
Agusan	03° 53' 15"	97° 25' 40"	1025	Primary lowland/ sub-montane rainforest.[2]
Gunung Kemiri	03° 49' 24"	97° 31' 05"	1000	Primary lowland rainforest.[3]
			1100, 1250	Primary lowland/ sub-montane rainforest.
			1400	Primary sub-montane rainforest.
Ketambe field station	03° 41'	97° 39'	500, 300	Primary lowland rainforest. [P]
Bukit Lawang	03° 32' 28"	98° 06' 53"	350, 250	Primary lowland rainforest. [P]
Lei Ekan	04° 01'57"	97° 34' 52"	1025	Primary lowland/ sub-montane rainforest.[4]
Lokop	04° 25' 14"	97° 31' 50"	450	Primary lowland rainforest.[5]

[1] Though within the GLNP there has been intensive illegal logging. Low canopy.
[2] Despite being in the GLNP, it is between two patches of *ladang*, and is likely to be cleared in the near future.
[3] Within 50 m of newly cleared *ladang* it is likely to be cleared in the near future.
[4] Less than one km from coffee garden, not protected.
[5] Slight disturbance near to where transect run but forest is protected.

Figure 3.2 Forest in MRT logging concession. View from logging camp. The transect was run in the circled area.

Figure 3.3 Leuser termite sampling team at MRT logging camp. From left, front row, Hasballah and Sugesti. Second from right, front row, Syaukani.

The sampling sites were not only widely dispersed geographically, but the LE is topologically highly variable. As the Leuser Ecosystem is split into three lowland areas by two mountain ranges, the investigation of environmental effects on assemblage structure had to take these into account. I identified three major environmental variables: *Position.* This was defined as east-west position according to the putative gene flow barriers of the two mountain ranges (i.e. west [0], central [1], east [2]). This was coded as a continuous variable. *Altitude.* Measured in metres. *Latitude* and *Longitude.* These were calculated using a GPS, except at Ketambe where we took the data from van Schaik & Mirmanto (1985). *Disturbance.* Forest types were divided into highly disturbed (large tree species absent, obvious signs of disturbance) and undisturbed or primary (large tree species present, no or slight sign of disturbance). Only one site (Krueng Baru) was highly disturbed.

Data analysis

I examined variation in species richness, feeding groups and species composition across the sites as follows:

Species richness and feeding groups. Multiple regressions were used to assess the influence of the environmental variables on species richness. I excluded disturbance level as a factor, as, with only one highly disturbed area, there were too few degrees of freedom for statistical significance to be assessed (but see Results).

Composition. Because there are many zero values in the dataset, a unimodal method of ordination analysis was appropriate. I used canonical correspondence analysis (CCA) to investigate the effect of each of the five environmental variables

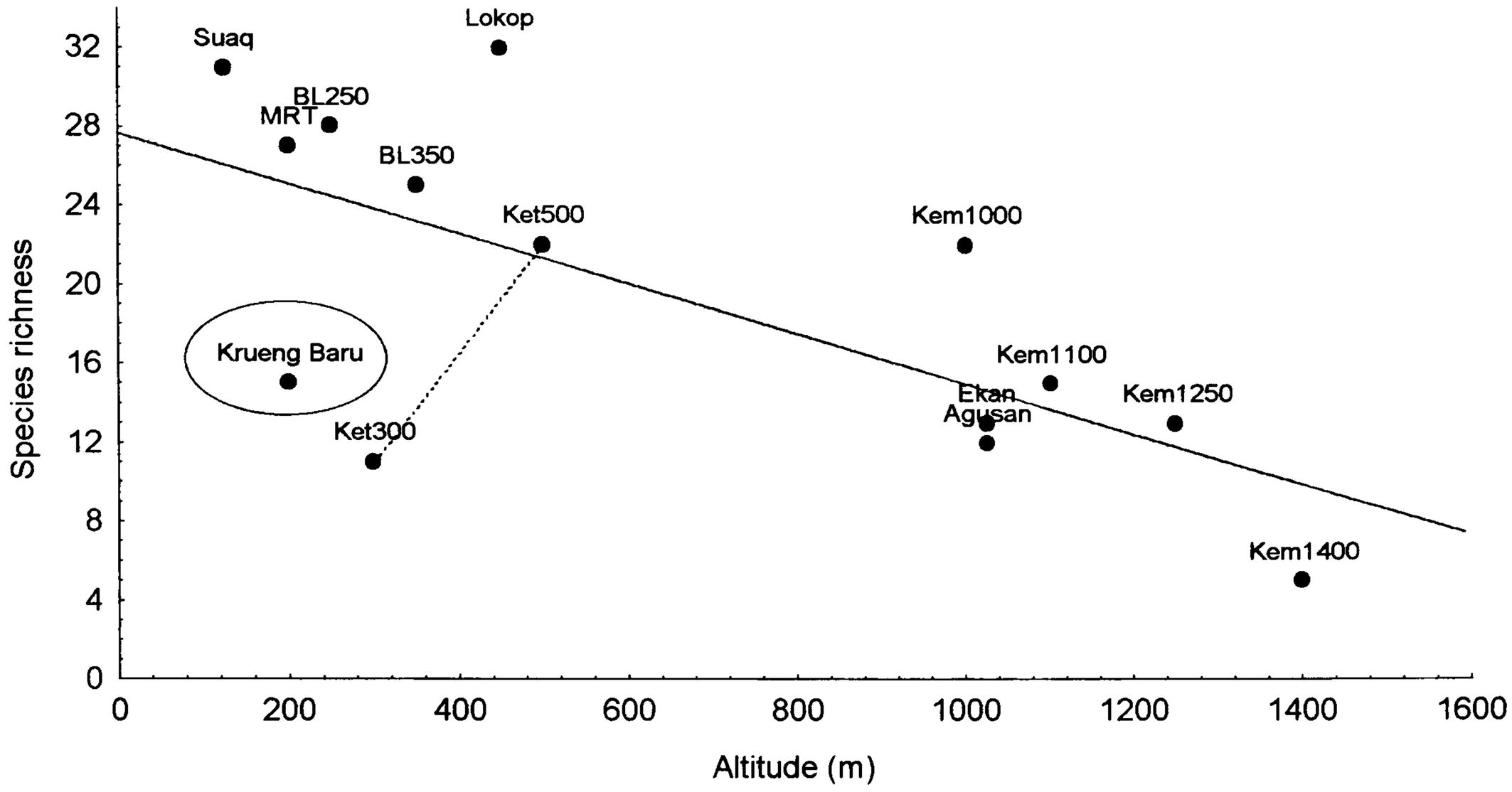
(latitude, longitude, position, altitude, disturbance) on species composition, using the CANOCO program. CANOCO uses a forward selection procedure to evaluate the importance of each environmental variable being tested. This procedure is similar to forward stepwise multiple regression. The analysis was initiated by testing the most influential environmental variable (the one with the highest marginal eigenvalue). This variable was then treated as a covariable ("partialled out") and the rest of the environmental variables were then tested, one by one in order of their importance (their conditional eigenvalues). This continued until no significant environmental variable remained in the matrix. The significance was tested at each step by a Monte Carlo permutation test with 999 permutations (ter Braak and Smilauer 1998).

In subsequent analyses only those environmental variables with conditional statistical significance in the above CCA were included.

3.3 Results

In total, I found 80 termite species in the Leuser Ecosystem. Of these, it is possible that seven are new to science (Appendix). I found termites of all feeding groups; though feeding group IV is represented in our collection by just one species (*Kemneritermes sarawakensis*) which was only found in one transect (Bukit Lawang, at 350 m). There was a strong correlation between the number of hits in a transect and the species richness in the same transect ($r^2 = 0.91$, $F_{(1,12)}$ 133, $P < 0.0001$). Therefore species richness and abundance show similar patterns. Multiple regressions showed that only altitude was significantly correlated with species richness ($r^2 = 0.46$, $P = 0.007$). As altitude increased, species richness and abundance decreased (Figure 3.4).

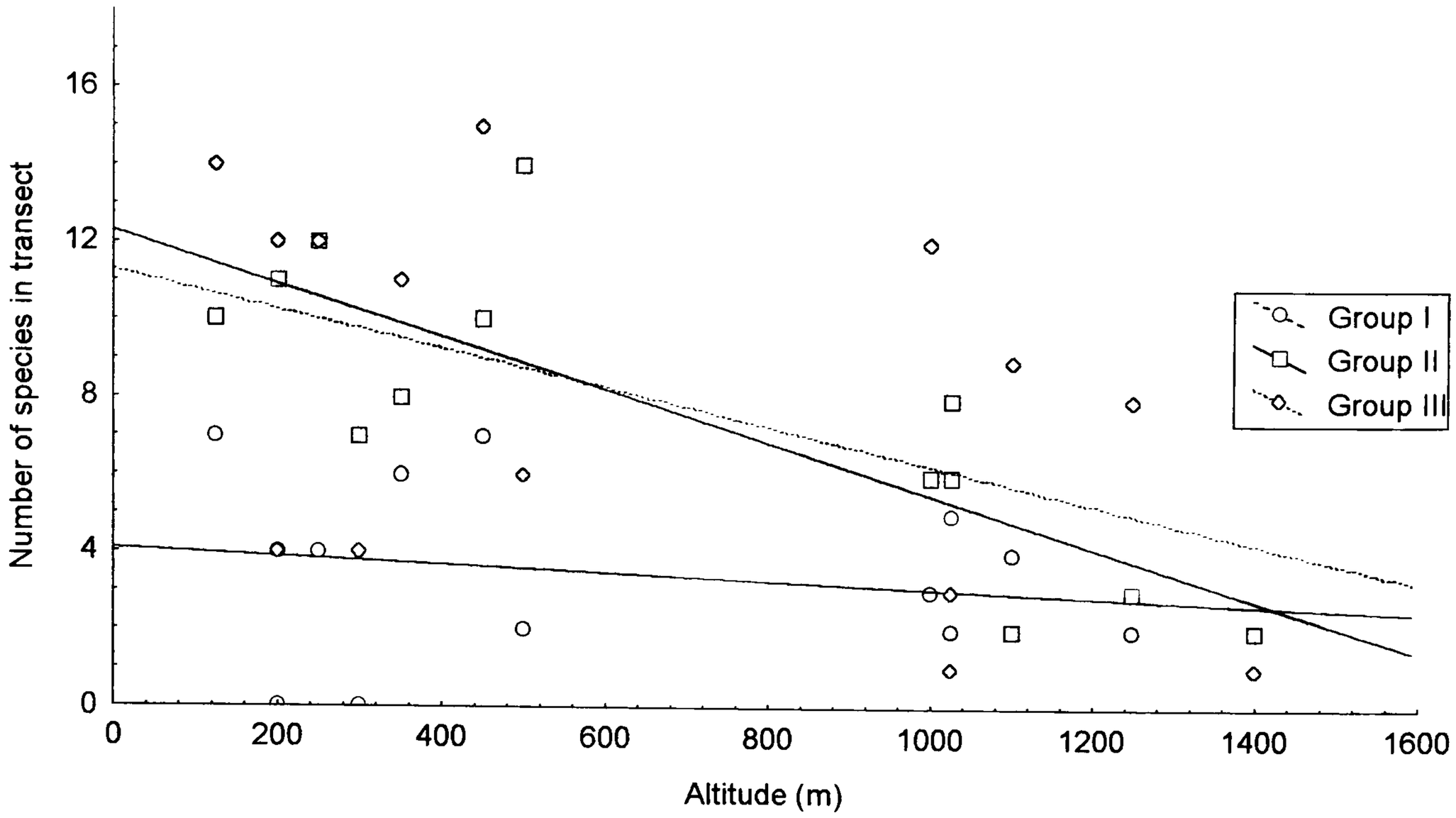
Figure 3.4. Influence of altitude on termite species richness in the Leuser Ecosystem, with a fitted regression line.
Codes: BL=Bukit Lawang, Kem=Kemiri, Ket=Ketambe



Multiple regression analysis of the feeding groups showed that termites from group II were significantly affected by increase in altitude ($r^2 = 0.7$, $P = 0.001$), group III feeders were marginally affected ($r^2 = 0.22$, $P = 0.09$), while group I feeders are unaffected ($r^2 = 0.04$, $P = 0.5$, Figure 3.5). None of the other environmental variables was significantly correlated with species richness or abundance.

Species-environment correlations indicate how good the fit was between the environmental variables and species-within-site data given these extracted axes. In this analysis, all were very high. The first four axes explained 49% of the total variance (inertia. Table 3.2).

Figure 3.5. Influence of altitude on termite feeding groups in the Leuser Ecosystem, with fitted regression lines



	Axis			
	1	2	3	4
Eigenvalues	0.474	0.368	0.245	0.437
Species-environment correlations	0.964	0.963	0.953	0

(Total inertia = 3.123)

Variable	Conditional eigenvalues	P-value	p-value of marginal eigenvalues
Altitude	0.43	0.001	0.001
Position	0.39	0.004	0.05
Longitude	0.27	0.176	0.05

Table 3.2. Summary results of the canonical correspondence analysis of the termite samples in the Leuser Ecosystem. See text for explanation.

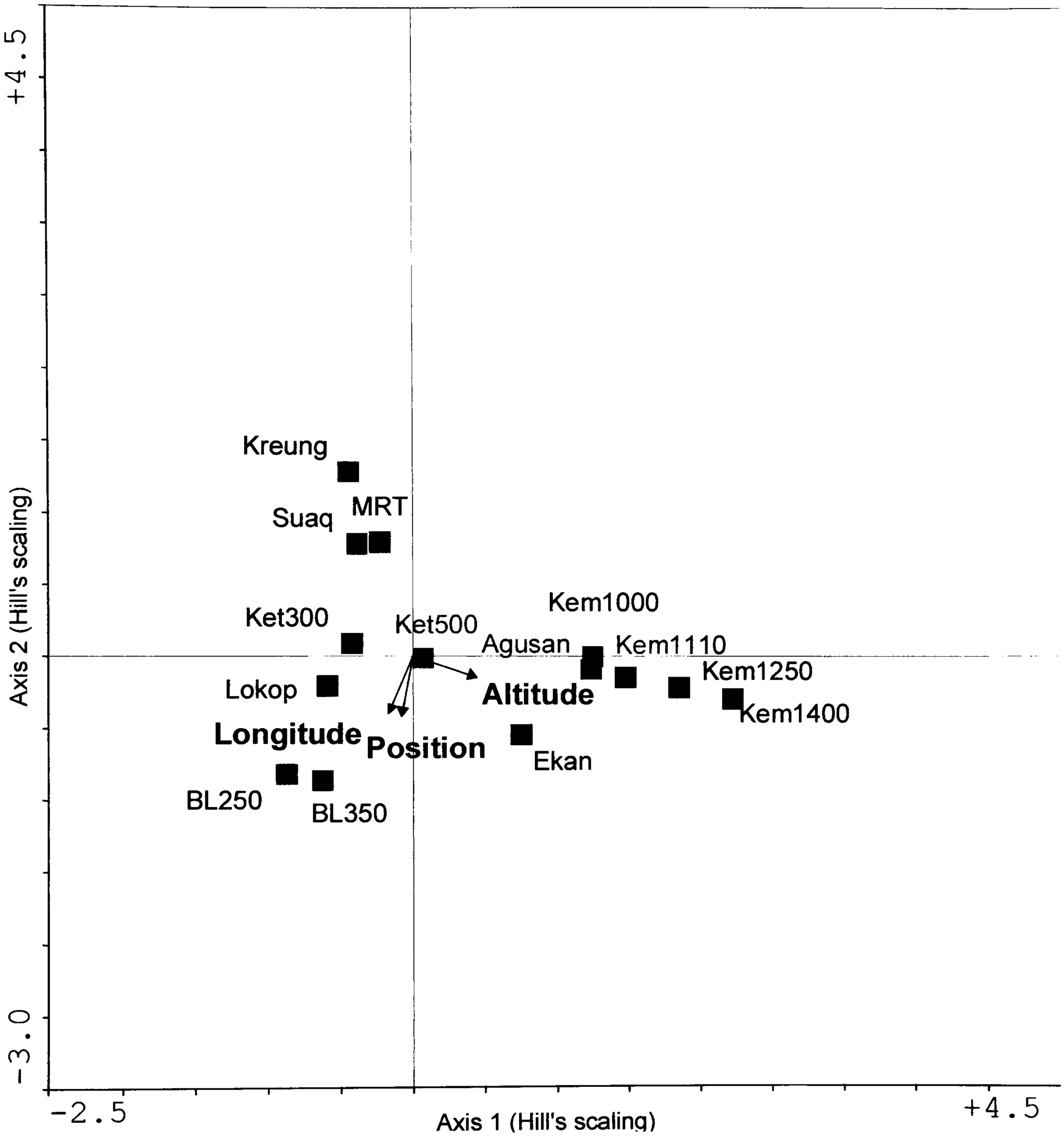
The P-values refer to statistical tests of the significance of the eigenvalues. In each case in a Monte-Carlo permutation test with 999 random arrangements was performed. Marginal eigenvalues are the same as conditional ones but without any environmental variable treated as a covariable.

The CCA site scatterplot (Figure 3.6) shows how the environmental variables (altitude, position and longitude) affect the termite composition of the different sites. The sites are clustered according to their altitude and position.

The CCA species scatterplot (Figure 3.7) showed that the fungus-growing termites (subfamily Macrotermitinae) were confined to low altitudes, while the other common subfamilies are present at all altitudes. Most species are found at low altitudes and a characteristic mid-altitude assemblage is evident (Figure 3.7).

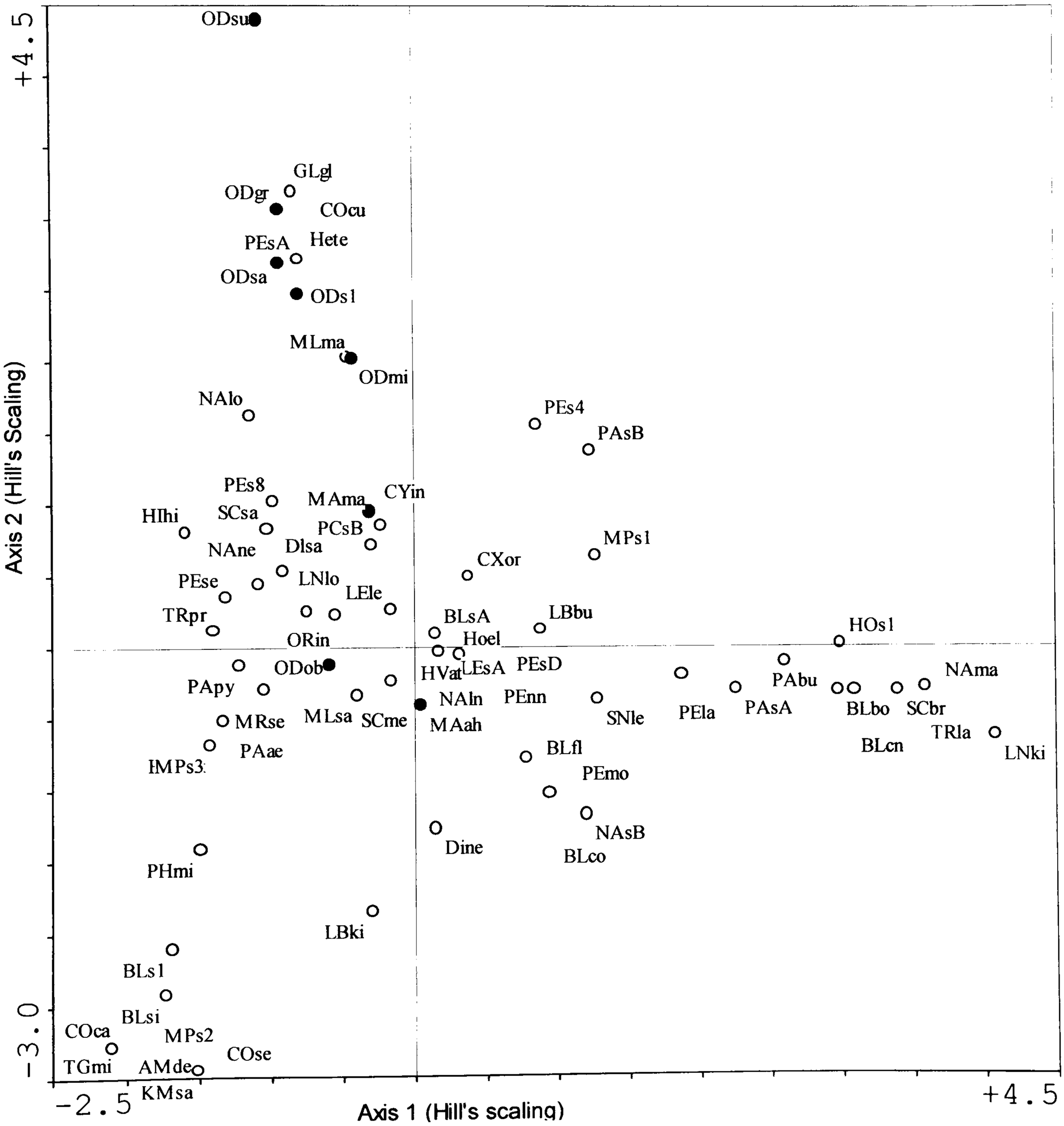
Position had a significant effect on termite species composition. The Macrotermitinae were rare at the east of the LE, while *Bulbitermes* spp. and *Prohamitermes mirabilis* were common. These in turn were rarer towards the west of the LE, while the Macrotermitinae are common. Compositional changes associated with position and longitude are closely correlated, though not identical, as the two mountain ranges do not run exactly north-south (Figures 3.6 & 3.7).

Figure 3.6 Ordination by study sites in the Leuser Ecosystem. Codes: BL = Bukit Lawang, Krueng = Krueng Baru, Ket= Ketambe and Kem = Kemiri



BIB. UNIV.

Figure 3.7 Ordination by CCA of termite species sampled in the Leuser Ecosystem (the species codes can be found in the Appendix). This is plotted on the same axes as figure 3. The Macrotermitinae (Filled circles) cluster towards the west.



3.4 Discussion

Altitude

For termites, it is clear that altitude is an extremely influential environmental variable and Figure 3.4 indicates that species richness and abundance drop with even a small (100 m) increase in altitude. On Gunung Mulu in Sarawak (Collins 1980) and Mount Giting-Giting in the Philippines (Thomas & Proctor 1997), termite abundance also decreased as altitude increased.

As altitude increases, so the mean temperature decreases (Whitten *et al.* 1984). The altitudinal ranges of all South East Asian termites are probably ultimately limited by temperature, as cool temperatures slow metabolic rates (Olson 1994). The altitudinal range of termites is greater on large mountains such as Gunung Mulu, where termites are found at 1,850 m (Collins 1980)-than on small ones such as Mount Giting-Giting - where the altitudinal limit for termites is below 1540 m (Thomas & Proctor 1997). This phenomenon can be explained by the Massenerhebung effect: the result of the tendency of fog to collect with increasing frequency with altitude (Grubb 1971, 1977; Grubb & Whitmore 1966). When there is fog, it reflects sunlight, reducing the ground temperature (Grubb & Whitmore 1966). Therefore the decrease in temperature with altitude occurs faster as fog becomes more permanent. Fog tends to collect at lower altitudes on small mountains than on large ones (Whitten *et al.* 1984).

The significant and nearly significant negative effects of altitude on termites of feeding groups II and III are probably a function of their feeding strategies. Group II termites nest either in the ground or in arboreal nests and travel to their easily assimilated, high energy (wood) food source. Those in group I tend to nest in and eat the same piece of wood (though some genera can form foraging trails to other pieces

ground and feed on surrounding humus or humified soils, both of which are lower energy sources than wood (Eggleton *et al.* 1998). Only group II termites are obligate foragers. With the decrease in mean temperature (and correspondingly lowered metabolic rates) with altitudinal increase, it is likely that foraging becomes energetically expensive. Foraging termites (group II) are therefore lost from the system before non-foragers (groups I and III). Group III termites, feeding on relatively low-energy humus, which has a higher cost of assimilation than wood (Eggleton *et al.* 1998), are probably pushed towards the lower limit of their energetic viability at higher altitudes.

Figure 3.8 Nest of *Lacessititermes*, an obligate forager.

No termite found in the Leuser is a mid or high-altitude (1000 m or above) specialist. At the generic level, all termites found at the higher sites are also found in

the lowlands. Even at species level (if one ignores the new species, the distribution of which cannot be certain, see below) there is no species found at high altitudes that is not also found at lower levels, either in this or in other studies (Eggleton *et al.* 1997, Thapa 1981, Tho 1992). However, a mid-altitude (c. 1000 m) assemblage is evident, consisting of species which, though found at lower altitudes, are at greater relative abundances at mid-altitude (Figure 3.7). These include *Parrhinotermes* sp A, *Schedorhinotermes brevialatus, Pericapritermes latignathus, Longipeditermes kistneri, Bulbitermes constrictoides* and *Nasutitermes matangensis*. These are termites that have wide environmental tolerances (they are found at higher altitudes, on the coast and in disturbed areas), so at mid-altitude, they can perhaps exploit the ecological space left by other species confined to the lowlands. The mid-altitude fauna has representatives of feeding groups I, II and III, and all the main clades (Kambhampati & Eggleton 2000) found in the LE; with the exception of the Macrotermitinae (which tend to be confined to drier areas, rather than the damper higher altitudes). A similar assemblage to this has also been found in the Maliau Basin in Sabah (Jones 2000).

Position

Position has a strong effect on species composition (Figures 3.6 and 3.7). Though we do not have detailed environmental data for each sampling site, in general the central valley and the western plain have less rain than the east (Blangpidie has 3405 mm y^{-1}, Ketambe, 3125 mm and Bukit Lawang, 4675 mm (van Beek 1996)). The Macrotermitinae are at a competitive advantage over other subfamilies in their feeding group in areas of low rainfall (Collins 1983, Davies 1997). This is probably why they

are more dominant in the west and the central valley (Figure 4) but are rare to the east. Macrotermitinae appear to be replaced by wood feeding Nasutitermitinae and Termitinae (chiefly *Bulbitermes* spp. and *Prohamitermes mirabilis*) in the eastern lowland sites.

Exceptions from the models

Two transects (those at Krueng Baru and at Ketambe, 300 m) are far below the regression line in Figure 3.4. Krueng Baru has fewer species than one would expect from its altitude probably because of the intensive illegal logging at the site. Though the transect was run within the GNLP, all of the large commercial trees have already been taken and logging still continues. The canopy height and density have been much reduced, probably allowing the temperature and humidity regime to fluctuate more than in primary forest. This may have removed those species of termites that cannot withstand such climatic fluctuations. A similar drop in species richness and abundance has been found in two forest types (one open forest, the other closed) in the Maliau Basin (Jones 2000) and over a disturbance gradient in Jambi, Sumatra (D. T. Jones, unpubl. data).

The Ketambe transect at 300 m also falls far below the regression line in Figure 3.4. It has a much lower species richness and abundance than the associated Ketambe transect at 500 m. This is probably due to flooding. The 300 m site is on flat land in the Alas valley. The river has occasionally flooded this area (Syaukani personal observations). It is probable that prolonged saturation of the soil would cause all of the soil-dwelling termites of that area to die. The termites found on this site may be those which have recolonised from upland areas.

In contrast, the transect at Lokop falls far above the regression line in Figure 1. The causes of this unusually high species richness are unknown. It may be that Lokop is showing the beginnings of a mid-altitudinal peak in diversity, as suggested for other groups by Olson (1994). However, as there was no reasonably accessible, undisturbed site between 500 and 1000 m altitude in the LE, I cannot test this hypothesis.

Taxonomy and biogeography

Of the seven species thought to be new to science collected in this study, it is unlikely that all of them are endemic to the Leuser Ecosystem. Most of these species are rare and in taxonomically difficult groups, so they may have been found in other sites and misidentified, or may be present in other sites but still awaiting discovery. Only one species, *Sabahitermes leuserensis* is common and widespread in the Ecosystem (collected 15 times from five sites).

The Leuser termite fauna is broadly typical of the Sunda region. All clades but one (the Apicotermitinae) of those found in Peninsular Malaysia (Jones & Brendell 1998) and Borneo (Eggleton *et al.* 1997) are present in the Leuser, and 80% of the Leuser species have been recorded elsewhere in the region (Abe 1984, Davies 1997, Eggleton *et al.* 1997, Gathorne-Hardy *et al.* 2000; Jones 2000, D. T. Jones, unpubl. data, Jones & Brendell 1998, Jones *et al.* 1998, Thakur 1976, Tho 1992). However, although the Leuser Ecosystem shares most of its species with other sites in the region, its wide variety of different termite assemblages (wet lowland, drier lowland, mid- and high-altitude) within one complete, unbroken ecosystem is unique. The Leuser Ecosysem is therefore of great conservation value and the above data re-emphasise its importance on both regional and global scales.

Appendix 3.1 Showing species found in Leuser Ecosystem

Species	Feeding group	Suaq	MRT	Krueng Baru	Bukit Lawang, 250m	Bukit Lawang, 350m	Ketambe, 300m	Ketambe, 500m	Lokop	Agusan	Ekan	Kemiri, 1000m	Kemiri, 1100m	Kemiri, 1250m	Kemiri, 1400m	Reference code
KALOTERMITIDAE																
Cryptotermes sp. nov. 1	I								1							CRS1
Cryptotermes sp.	I					1										CRs?
Glyptotermes paratuberculatus Thapa	I								1							GLpa
RHINOTERMITIDAE																
Heterotermitinae																
Heterotermes tenuior (Haviland)	I	2														Hete
Coptotermitinae																
Coptotermes kalshoveni Kemner	I				4											COca
Coptotermes sepangensis Krishna	I					2										COse
Coptotermes borneensis Oshima	I								1							CObo
Coptotermes curvignathus Holmgren	I	1														COcu
Termitogetoninae																
Termitogeton planus Thapa	I				1											TGmi
Rhinotermitinae																
Parrhinotermes pygmaeus Holmgren	I	2				2										PApy
Parrhinotermes sp A Tho	I	2				1		1	1	2		1	3	4	2	PAsA
Parrhinotermes sp B Tho	I		1							1						PAsB
Parrhinotermes buttel-reepeni Holmgren	I	1								2	1		1		1	PAbu
Parrhinotermes aequalis (Haviland)	I	1	3		3	3			2							PAae
Schedorhinotermes brevialatus (Haviland)	I									7		1	9	1		SCbr
Scedorhinotermes sarawakensis (Holmgren)	I		2						3							SCsa
Schedorhinotermes medioobscurus (Holmgren)	I	12	12		15	10		4	6	4	1	3	1			SCme
TERMITIDAE																
Termitinae																
Globitermes globosus (Haviland)	II	12	10	6												GLgl
Prohamitermes mirabilis (Haviland).	II		6		22	26			5							PHmi
Amitermes dentatus Holmgren	II				1											AMde
Microcerotermes serrula (Desneux)	II	3	3		3	2			10		1					MRse
Termes propinquus (Holmgren)	III	2	1		4											TRpr
Termes laticornis (Haviland)	III												2			TRla
Pericapritermes latignathus (Holmgren)	III		1				3				2	6	2	1		PEla
Pericapritermes sp.D (Tho)	III	13		2	4	2	2		13		1	7	2	4		PEsD
Pericapritermes nr. nitobei	III	2	2		2	1			2				2	2		PEnn
Pericapritermes mohri (Kemner)	III								2	1	3					PEmo
Pericapritermes sp.4	III	3												1		PEs4
Pericapritermes speciosus (Haviland)	III											1				PEpr
Pericapritermes semarangi (Holmgren)	III	7	1		3				7							PEse
Pericapritermes sp. A (Homa)	III	3	1													PEsA
Pericapritermes sp.8	III		1						1							PEs8
Dicuspiditermes nemorosus (Haviland)	III	1			7	7			5			1	16			Dine
Dicuspiditermes santschii (Silvestri)	III		2			1										Dlsa
Pseudocapritermes orientalis (Ahmad and Akhtar)	III	5	5	2	6		1	1	2			10		5		CXor
Procapritermes sp. B	III	2	12	1	4	1						1		1		PCsB
Procapritermes sp. 1	III	1	2					6				1			2	MPs1
Procapritermes sp. 2	III				1											MPs2
Procapritermes sp. 3	III								1							MPs3
Homallotermes eleanorae Krishna	III							1								Hoel
Homallotermes exiguus Krishna	III								1							HMex
Kemneritermes sarawakensis Ahmad and Akhtar	IV					12										KMsa
Labritermes buttelreepeni Holmgren	III	2			1							6				LBbu
Labritermes emersoni Khrisna and Adams	III					1										Laem
Labritermes kistneri Khrisna and Adams	III				3	3			1			1	1			LBki
Macrotermitinae																
Macrotermes ahmadi Tho	II	2				3						2				MAah
Macrotermes malaccensis (Haviland)	II	9	6	8		3	6	11	3		2	5				MAma
Odontotermes grandiceps (Holmgren)	II		1	4			1									ODgr
Odontotermes sarawakensis (Holmgren)	II	10	6	6			3	1								ODsa
Odontotermes oblongatus (Holmgren)	II			3	5		6	2			3					ODob
Odontotermes minutus Amir	II	1	3					1								ODmi
Odontotermes billitoni (Holmgren)	II			2												ODsu
Odontotermes sp. 1	II	2														ODs1
Nasutitermitinae																
Nasutitermes matangensis (Haviland)	II									4				2		NAma
Nasutitermes longinasoides Thapa	II							3								NAln
Nasutitermes longinasus (Holmgren)	II		4	2	2											NAlo
Nasutitermes johoricus (John)	II							3			10					NAsB
Nasutitermes neoparvus Thapa	II	3		1	4		2	2								NAne
Nasutitermes atripennis (Haviland)	II							1								HVat
Sabahitermes leuserensis (Gathorne-Hardy)	III							5	2			1	1	1		SNle
Malaysiotermes holmgreni (Ahmad)	III	6			5	1	2	3	3				1	1		MLsa
Malaysiotermes spinocephalus Ahmad	III			6					2			1				MLma
Oriensubulitermes inanis Ahmad	III	12	17		4	7		2	2			4				ORin
Leucopitermes leucops (Holmgren)	III	1	1			1			1				1			LEle
Leucopitermes sp A	II							7								LEsA
Ceylonitermes indicola Thakur	II			5					3		3					CYin
Hirtitermes hirtiventris Holmgren	II			1	1											HIhi
Bulbitermes singaporiensis (Haviland)	II				13	14			3							BLsi
Bulbitermes constrictoides (Holmgren)	II							2		10			6		2	BLcn
Bulbitermes flavicans (Holmgren)	II		1		1			1			5	1				BLfl
Bulbitermes borneensis (Haviland)	II											1				BLbo
Bulbitermes sp A (David)	II	25	12	2	2	9	2	9	25	2	14	3	3	1		BLsA
Bulbitermes sp.1	II				25	16			26							BLs1
Bulbitermes constrictus (Haviland)	II							1			5					BLco
Lacessititermes pilferus (Holmgren)	II								1							LCs1
Lacessititermes cuphus (Silvestri)	II									1						LCsA
Hospitalitermes sp 1	II									1						HOs1
Hospitalitermes umbrinus (Haviland)	II								8							HOum
Longipeditermes longipes (Haviland)	II	10	6		2	4	7	7	4	1						LNlo
Longipeditermes kistneri Akhtar and Ahmad	II											7		3	3	LNki
Total No. Spp.		31	27	15	28	25	11	22	32	12	13	22	15	13	5	

TAXONOMIC WORK

A part of this chapter has been published as: Gathorne-Hardy F.J. **2001**. A review of the South-East Asian Nasutitermitinae (Isoptera: Termitidae), with descriptions of one new genus and a new species and including a key to the genera. *Journal of Natural History* 35: 1485-1506.

Other parts of the chapter have been submitted to the *Journal of Natural History* as: Gathorne-Hardy F.J. The termites of Sundaland: Their taxonomy and faunistics, including thirteen species and three genera synonomised, and a new species described, a key to the soil-feeding Nasutitermitinae and a species checklist.

4.1 Introduction

The termites of the Sunda region (Sumatra, Borneo, Java, the Malay peninsula-up to the isthmus of Kra-and associated islands) have recently received a very high collecting effort. From 1994-2001 researchers from The Natural History Museum, University of Malaysia, Sabah, Syiah Kuala University, Banda Aceh and the Bogor Museum have collected a very large number of Sundan termites, and N.M. Collins and R.D. Buxton collected many specimens as part of Project Wallace in Sulawesi.

The soil-feeding Nasutitermitinae of Southeast Asia were revised by Ahmad (1968) but since then there has been confusion as to the limits of his genera (Tho, 1982, 1992, Collins, 1984). Ahmad did not include a key in his publication, and it appears that he did not fully appreciate the level of intra-specific variation found in

the Nasutitermitinae. The taxonomy of the wood and epiphyte-feeding Nasutitermitinae is also difficult, with many poorly defined genera. In this chapter I aim to make clearer the species and generic limits of some of the termites of the region, as well as reviewing the Nasutitermitinae and providing a key to the genera (and to the species of soil-feeding Nasutitermitinae). I also plan to describe a new genus found in the Leuser Ecosystem (Sumatra, Indonesia), a new species of *Hirtitermes* Holmgren from Sulawesi, the major soldier of *Ceylonitermes indicola* Thakur and a new species of *Leucopitermes* Emerson.

4.2 Taxonomic discussion

Rhinotermitidae

Schedorhinotermes

S. sarawakensis

Tho (1992, p. 75) separated *S. sarawakensis* (Holmgren) and *S. malaccensis* (Holmgren) only on an arbitrary size difference; *sarawakensis* has a head length of greater than 2.20mm(major soldier) and 1.20mm (minor soldier), while *malaccensis* has a head length of less than 2.20 mm (major soldier) and 1.20mm (minor soldier). However, as Tho says, these species are highly variable, and I have found specimens from the same colony with measurements of both greater than and less than 2.20mm in the major soldier and 1.20 mm in the minor soldier. It is effectively impossible to separate these two species. *S. sarawakensis* therefore becomes a junior subjective synonym of *S. malaccensis.*

S. javanicus

Thapa (1981) separates *S. javanicus* Kemner and *S. medioobscurus* (Holmgren) by the relative lengths of the antennal segments. I have examined a

very long series of *Schedorhinotermes* and have never been able to split these two species on an antennal character, or any other. Tho (p. 76) states that they share all of their diagnostic characters. He too was unable to separate these two species. Therefore I consider *S. javanicus* to be a junior subjective synonym of *S. medioobscurus*.

S. tarakanensis

S. tarakanensis (Oshima) has been separated from *S. medioobscurus* by being smaller (Thapa 1981, Thakur & Thakur 1992). I have found many specimens of intermediate size and have therefore not been able to split these two species. I consider *S. tarakanensis* to be a junior subjective synonym of *S. medioobscurus*.

Termitogeton

T. planus

Thapa (1981, p.89-91) erected the species *Termitogeton minor* on the basis that it is "much smaller" than *T. planus* (Haviland). However, in his published size ranges, *T. minor's* head is only 0.05 mm shorter and 0.01mm narrower than that of *T. planus*. I do not consider that Thapa had taken sufficient account of intra-specific size variation and I therefore consider that these two species are really only one. *T. minor* is the junior subjective synonym of *T. planus*. Jones *et al.* (1998) are also of this opinion.

Prorhinotermes

Following Tho (1982, 1992) and Gathorne-Hardy *et al.* (2000), I consider that all of the *Prorhinotermes* found in the Sunda region are all one species, *P. flavus.*

Macrotermitinae

Odontotermes

O. sundaicus

O. sundaicus (Kemner) and *O. billitoni* (Holmgren) have very similar descriptions. Kemner (1934, p. 99) discusses the similarity of the two species, stating that the main difference between them is the relative lengths of the 3rd and 4th antennal segments. This character is an unreliable one with which to separate species, as these two antennal segments are often incompletely divided (Pers. obs). I have not been able to use this character to successfully separate the two species.

I have examined a long series of *O.sundaicus* from Sumatra, Java and Borneo. These, as well as matching the type specimen of *O. sundaicus*, also match the description of *O. billitoni.* It therefore seems very probable that these two species are the same. I therefore consider that *O. sundaicus* is a junior subjective synonym of *O. billitoni.*

O. mathuri

O. mathuri Thapa and *O. minutus* Amir also have identical descriptions. Having examined a long series of termites which match the descriptions of both, it seems very likely that they are the same species, making *O. mathuri* a junior subjective synonym of *O. minutus*.

Termitinae

Termes

T. borneensis and *kalumpangensis*

Thapa (1981) erected the species *T. borneensis* and *kalumpangensis*, which were separated from *T. comis* Haviland by the shape of the frontal projection (p. 179 & 180). However, Tho (1982, PhD thesis p. 198) says that the frontal projection of *T. comis* shows great intra-specific and intra-colony variation. I too have found this to be so. I have examined 20 series of *T. comis*, and have found that the rostrum shape varies considerably, to the point where it looks like both *kalumpangensis* and *borneensis.* I have found that it is impossible to separate these species on rostrum character, and the size range of *comis* encompasses the other two species. As all other characters in the description match those of *comis* I think that both *borneensis* and *kalumpangensis* are junior subjective synonyms of *comis.*

Pericapritermes

Pericapritermes species are very hard to separate. Homathevi (PhD thesis) has used two characters (tips of mandibles and enteric valve characters) which divide the genus into two groups. After that the species are separated by using head and mandible size. Having examined more than 400 series of *Pericapritermes*, I have found that instar polymorphism is common. Mandible: head length ratios are not stable within a colony.

P. paraspeciosus

Pericapritermes paraspeciosus Thapa (p. 216-218) was separated from *P. speciosus* (Haviland) on the basis that it has a narrower head, shorter mandibles

and fourteen antennal segments. The head width of *paraspeciosus* is only 0.03 mm narrower than *speciosus*, Haviland (p. 413) described *speciosus* as having 14 antennal segments and (as above) the mandible size is variable. Therefore I think that *P. paraspeciosus* is not a valid species and is a junior subjective synonym of *P. speciosus*.

Coxocapritermes and _Pseudocapritermes_.

The genus *Coxocapritermes* was erected by Ahmad and Akhtar (1981). It was separated from other genera (particularly *Pseudocapritermes*) by the following characters:

1. The soldiers and workers of *Coxocapritermes* all have a hump on their fore coxae. No other genus does.
2. The soldier of *Coxocapritermes* has a V-shaped labrum (U-shaped in *Pseudocapritermes*).
3. The enteric valve of *Coxocapritermes* workers has no scales on the cushions, while there are a few spined scales on those of *Pseudocapritermes*.

However, I have found that these characters are either more variable than Ahmad and Akhtar (1981) appreciated or are not robust enough to separate the two genera.

I have found that the hump on the fore coxa varies in extent and visibility and I have found specimens from Sumatra which have both a hump on the fore coxa and spined scales on the enteric valve. Clearly these specimens come intermediate between *Coxocapritermes* and *Pseudocapritermes,* and demonstrate that it is impossible to separate the two genera using these characters. The shape of the labrum (V-shaped in *Coxocapritermes* as opposed to U-shaped in

Pseudocapritermes) is a character that is difficult to use. The difference between a V and a deep U is difficult to define and having examined a long series of *Coxocapritermes* and *Pseudocapritermes* I have found that when using this character I cannot split the two genera.

As I have found it impossible to effectively separate the two genera, I consider *Coxocapritermes* to be a junior subjective synonym of *Pseudocapritermes*. Therefore *Coxocapritermes orientalis* becomes *Pseudocapritermes orientalis.*

Procapritermes* and *Malaysiocapritermes

Malaysiocapritermes, another genus erected by Ahmad and Akhtar (1981) was separated from *Procapritermes* by the following characters:

1. The soldiers and workers of *Malaysiocapritermes* have tibial spurs 2:2:2 (*Procapritermes* 3:2:2).
2. The left worker mandible of *Malaysiocapritermes* has the apical tooth separated from the first marginal by "a distance slightly greater than the distance separating the ...first...marginal tooth from the third marginal tooth, whereas in *Procapritermes* ...the left...apical [tooth is] separated from the ...first...marginal tooth by a distance which is one-and-a-half times the distance between the third marginal tooth and...first...marginal tooth. In the right mandible of *Procapritermes* the apical tooth is more widely separated than in *Malaysiocapritermes*" (Ahmad & Akhtar 1981, p. 9).
3. The enteric valve of *Malaysiocapritermes* is very similar to that of *Pseudocapritermes*, with a few spines in a ring at the posterior end and spiny scales on the cushion. That of *Procapritermes* is very different, with two types

of scales on the cushion, one type with comb-like spines, one with normal spike-like spines.

However, I have found that these characters are either more variable than Ahmad and Akhtar (1981) appreciated or are not robust enough to separate the two genera.

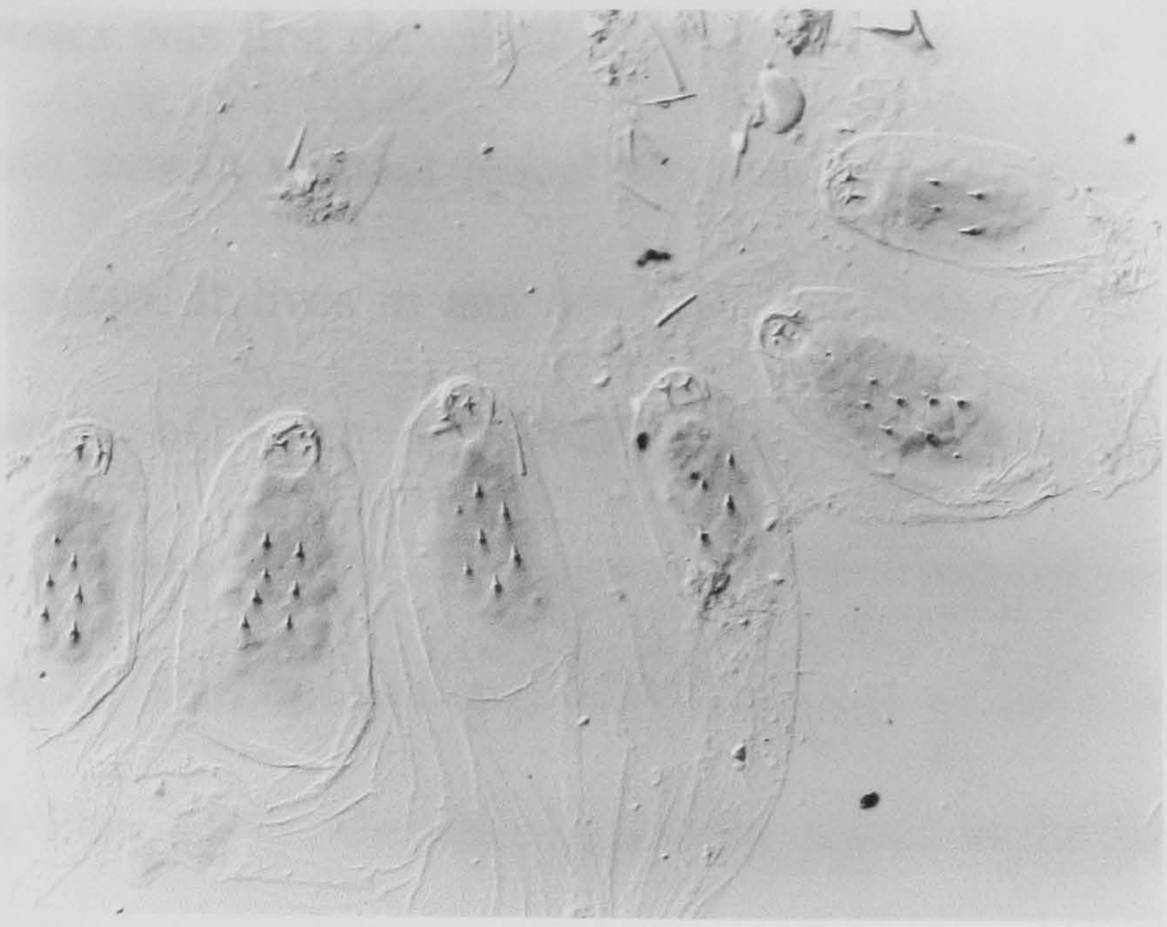
1. I have found both soldiers and workers of paratypes of *Malaysiocapritermes prosetiger* (Ahmad) and from other collections with tibial spurs 3:2:2. The number of tibial spurs on the front legs shows intra-colony variation, with some specimens having three and some two. As the number of tibial spurs is not intra-colony consistent it is not a good character for separating genera.
2. I have examined the worker mandibles of paratype material of the type species *M. holmgreni* (Ahmad), and those of the type species of *Procapritermes, P. setiger* (Haviland), as well as a long series of other *Procapritermes* and *Malaysiocapritermes* species I have found that the worker mandible characters are variable; that there is such intra-generic variation that I have not been able to separate these two genera using the worker mandibles.
3. I have found intermediates between the two described enteric valve morphologies. *P. neosetiger* Thapa and *M. prosetiger* both have very similar enteric valves, with one or two comb-like spines, and the rest very similar to those of *Malaysiocapritermes*.

With all the characters which should separate *Malaysiocapritermes* and *Procapritermes* I have either found intermediates or that they are not robust enough in order to be able to split the two genera.

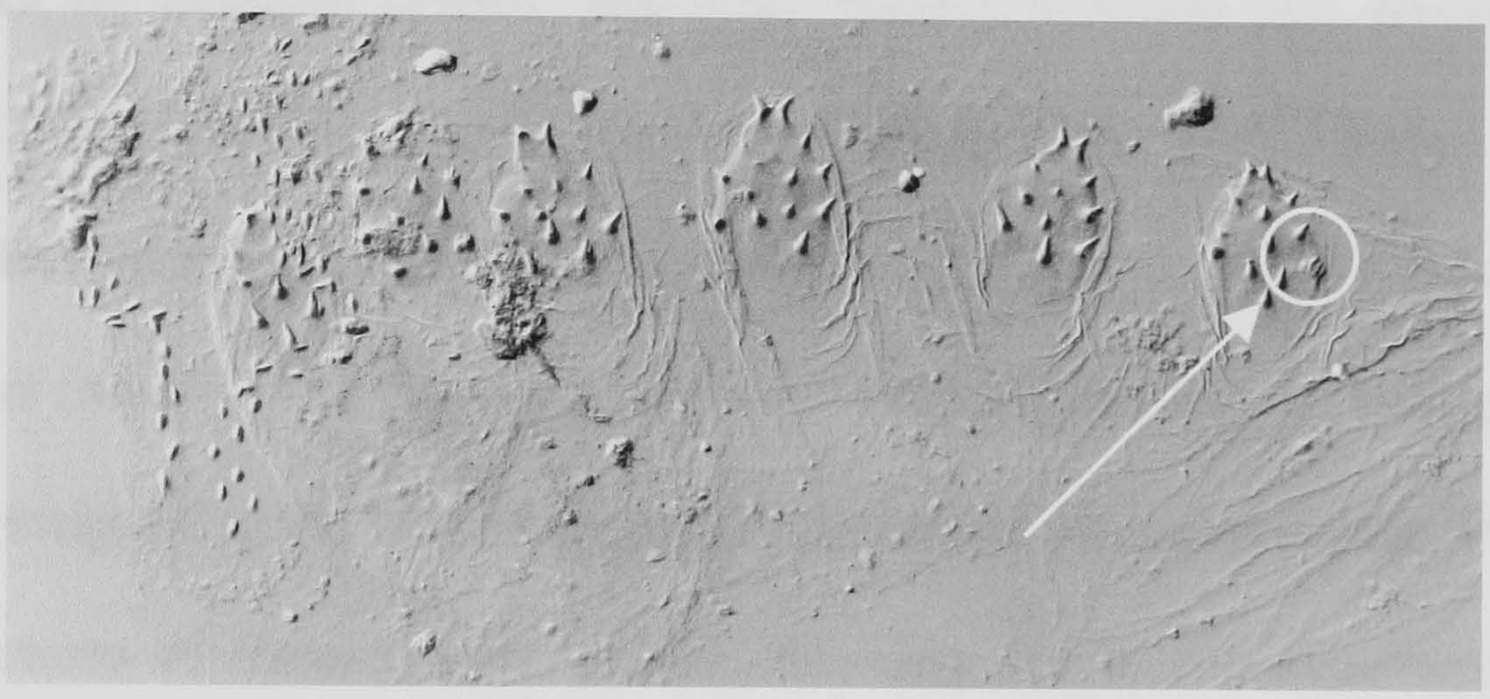
I therefore consider *Malaysiocapritermes* to be a junior subjective synonym of *Procapritermes*.

M. holmgreni, longignathus and *prosetiger* are now *Procapritermes* species.

A



B



C

Figure 4.1
Showing the intermediates in the two enteric valve morphologies.
A: with just spines. B: with spines and a comb (circled) and C: with spines and combs

1 micron

The position of the South East Asian *Subulitermes*-group

Subulitermes was first described from soldier material by Holmgren (1911) as a small nasute termite without apical processes on the mandibles and with a cylindrical, thin nasus. It lives in and feeds on soil in south America. Since then several new genera of Asian soil-feeding Nasutitermitinae have been erected (Emerson, 1960, Ahmad, 1968). These genera all have similar soldier morphology and living habits to *Subulitermes* and were assumed to be closely related to it (Emerson, 1960, Tho, 1992). They were therefore placed in the *Subulitermes*-group of genera by Emerson (1960), and other authors followed this precedent (e.g. Ahmad, 1968, Tho, 1992, Eggleton *et al.* 1997, Jones & Brendell, 1998).

The gut morphology of the worker caste contains many important taxonomic characters (Sands, 1972, Roisin & Pasteels, 1996) and this has not been previously fully investigated in the South East Asian soil-feeding Nasutitermitinae. The worker gut structures of these species indicate that they are in the *Nasutitermes*-group (Roisin & Pasteels, 1996) rather than the *Subulitermes*-group. *Subulitermes* has a short first section of the proctodeum (P1) and no mixed segment at the mesenteric-proctodeal junction. The South East Asian soil-feeding genera all have a very long P1 and a mixed segment. The *Subulitermes*-group of humivorous Nasutitermitinae is absent from South East Asia, New Guinea (Roisin & Pasteels, 1996) and Madagascar (Eggleton, unpublished data) but is found in Australia (Miller, 1984), the Neotropics (Mathews, 1977) and Africa (Eggleton *et al.*, 1995).

The major soldier of *Ceylonitermes indicola*

A species of Nasutitermitinae which has dimorphic soldiers was collected from the Leuser Ecosystem in Sumatra. The minor soldiers and the workers match

Ceylonitermes Holmgren specimens in the BMNH collection. I have therefore assigned these specimens to *Ceylonitermes*. The minor soldiers and workers match the description of *C. indicola* (Thakur, 1976) and therefore I assume that the Leuser specimens are *C. indicola.* It is probable that the soldier dimorphism was not recognised by Holmgren (1912) or later authors (i.e. Thakur, 1976, Collins, 1984) if in each case only a few termites were collected. The minor soldiers are more aggressive than the major soldiers and may be more numerous (Tho, 1992, author's personal observations). Therefore minor soldiers tend to be collected in greater numbers (in the collection from the Leuser Ecosystem, less than half of the series collected contained major soldiers).

Tho (1982, 1992) described what he called an undescribed new genus of Nasutitermitinae (Genus A). Although I have not examined Tho's material as it is lost(Laurence Kirton pers. comm.) from his description and illustrations I consider his Genus A species A to be a new species of *Ceylonitermes.*

Aciculioiditermes, Proaciculitermes* and *Malaysiotermes

Ahmad (1968) erected the genera *Malaysiotermes, Proaciculitermes* and *Aciculioiditermes* on the basis of the dentition of the worker mandibles. They were separated from each other by the relative lengths of the apical tooth, the prominence of the third marginal tooth of the left mandible and the number of ridges on the left molar plate. The soldiers were separated by size, the amount of hair on the head and the length of antennae. Since the time of Ahmad's descriptions termites have been found which have worker mandible characters intermediate between those described for *Malaysiotermes*, *Proaciculitermes* and *Aciculioiditermes.* When I examined a

long series of specimens, the subtle worker characters Ahmad used to separate these three genera overlapped. The worker mandibles and gut structures of the paratypes of these three genera are very similar; I have not been able to separate them effectively using worker characters.

The soldier of *Malaysiotermes* was separated from *Aciculioiditermes* and *Proaciculitermes* by the presence of "long bristles on the head and...long antennae" (Ahmad, 1968, p 7). I do not consider that "long antennae" (Ahmad was not clear about how long these antennae are, but from his illustration on p. 7 and from the paratype material, it appears that they are not significantly longer than those of any other soil-feeding nasute termite) and "bristles" (which are not very thick or conspicuous on the paratype material) constitute a characteristic enough difference from other genera to justify *Malaysiotermes* having separate generic status.

Aciculioiditermes soldiers were separated from *Proaciculitermes* by Ahmad (1968) by size and the density of hair on the head (p 9). However, his measurements of the holotypes of *P. malayanus* and *A. holmgreni* have the same head length with rostrum (1.38 mm) and less than 0.05 mm difference for the other measurements. I think that size therefore cannot be used to separate these two genera. As for the other soldier characters, I do not consider that differences only in the density of setae on the soldier head and the relative length of the second and third antennal segments (pp. 10 and 22) are enough to justify the status of *Proaciculitermes* and *Aciculioiditermes* as separate genera.

Malaysiotermes has page priority (Ahmad, 1968, page 6) over *Proaciculitermes* and *Aciculioiditermes* (Ahmad, op. cit. pages 8 and 19 respectively) so I consider *Aciculioiditermes* and *Proaciculitermes* to be junior synonyms of *Malaysiotermes*.

Malaysiotermes

Malaysiotermes (=*Aciculioiditermes*) *holmgreni*, *M. denticulatus* and *M. sarawakensis* (Ahmad, 1968, pages 19, 22 and 23 respectively) were separated from each other by the following soldier characters: 1. The presence and absence of denticle-like protuberances at the base of the rostrum, 2. the presence or absence of minute points on the mandibles and 3. the relative hairiness of the tip of the rostrum. I have examined paratypes of these species, as well as specimens from Sumatra and Sabah. The published measurements of the three species are very similar and overlap. I have found colonies of *Malaysiotermes* in which some soldiers have pronounced denticle-like protuberances at the base of the rostrum, while on other specimens from the same colony they are reduced; showing that there is considerable intra-specific (and intra-colony) variation of this character. The presence or absence of points on the mandibles of Nasutitermitinae soldiers also shows much intra-specific variation. (personal observations, Tho, 1992, Hoare & Jones, 1998) and is not a reliable character with which to separate species (Hoare & Jones *op. cit.*). From the paratype specimens in the NHM and Ahmad's descriptions the difference in the density of hairs on the rostrum of *M. sarawakensis*, *holmgreni* and *denticulatus* is very small; almost not discernible. As the distinguishing characters of these three species either overlap or are extremely variable, I consider *M. denticulatus* and *M. sarawakensis* to be junior synonyms of *M. holmgreni* (which has page priority).

Malaysiotermes spinocephalus, lowi, sabahensis, malayanus and *orientalis* were all separated from one another by the presence or absence of denticle-like protuberances on the rostrum, the relative size of the hump (when seen laterally) on

the base of the rostrum, the size of the head, the relative lengths of antennae and the amount of hair on the head (Ahmad 1968, pp. 6, 11,14, 17, 18).

As above, the denticle-like protuberances show intra-specific variation so are not good characters. I have examined *c.* 150 series of *Malaysiotermes* and the relative size of the hump (when seen laterally) on the base of the rostrum shows intra-colony variation, so it is not a good character for separating *Malaysiotermes* species. I have examined paratype material of all of the above species, closely examining the amount of hair on the head, the size and the relative lengths of the antennae and have not been able to separate them.

As *M. spinocephalus* has page priority (p. 6), I consider that *M. lowi, sabahensis, malayanus* and *orientalis* are all junior subjective synonyms of *M. spinocephalus.*

Subulioiditermes

S. major

Thapa (1981, pp.367 & 368) described *Subulioiditermes major*. In his description he states that it come close to *S. subulioides* Ahmad, but has a larger head and a longer rostrum. However, the ranges of both the head and the rostrum overlap (see Ahmad, p. 3 & Thapa p. 368). Therefore it is very likely that *S. major* is not a valid species, but is a junior subjective synonym of *S. subulioides.*

Nasutitermes matangensiformis

N. matangensiformis was erected by Holmgren (1913) on the basis that the soldier is smaller than *N. matangensis* (Haviland). Since then intermediates between the two size ranges have been discovered (see table 1). As all other morphological

characters and the natural history of the two species are the same (Holmgren, 1913, Roonwal, 1969, personal observations) I consider them to be only one species. Therefore *N. matangensiformis* becomes a junior synonym of *N. matangensis.* For the same reasons, Roonwal and Sen-Sarma (1956) also considered that *N. matangensiformis* is a junior synonym of *N. matangensis*. However, since they synonomised the two species, *N. matangensiformis* had been re-erected by both Ahmad (1958, 1965) and Thapa (1981). Neither author gave a reason for re-erecting *N. matangensiformis*, though both of them refer to Roonwal and Sen-Sarma's 1956 paper, in which the two species were synonymies. I have examined paratype material of *N. matangensis* (BMNH No. 358) as well as other material identified by Holmgren. I have also examined *N. matangensiformis* from the BMNH collection and specimens of *N. matangensis* collected from the Krakatau islands.

Table 4.1. Showing measurements of *N. matangensis* and *matangensiformis*

Nasutitermes matangensis	Head length	Head width
Paratype. BMNH 358	1.91-2.07	1.39-1.50
Det. Holmgren BMNH 1899-41	1.93-1.95	1.33-1.47
Ahmad (1958)	1.95-2.09	1.24-1.37
Thapa (1981)	1.95-2.05	1.27-1.42
Thakur & Thakur (1992)	1.75-2.00	N/A
Ex. Panjang, Krakatau Is	1.69-1.81	1.12-1.87
Ex. Rakata, Krakatau Is	1.71-1.79	1.2-1.26
Nasutitermes matangensiformis		
Holmgren (1913)	1.67	1.1
Ahmad (1958)	1.67-1.74	1.04-1.11
Ahmad (1965)	1.61-1.89	1.04-1.27
Thapa (1981)	1.61-1.77	1.02-1.05
Coll. Light	1.59-1.69	1.06-1.09
BM 1965-152	1.78-1.89	1.05-1.15

History of *N. matangensiformis* publications

1898. *Termes matangensis,* Haviland, J. Linn. Soc. London, 26. pp. 427-428.

1913. *Eutermes (Eutermes) matangensiformis*, Holmgren, K. svenska Vetensk. Akad. Handl., 50 (2) p. 185.

1949. *Nasutitermes matangensiformis*, Snyder, Smithson. misc. Coll., 112, p. 286.

1956. *Nasutitermes matangensis matangensiformis*, Roonwal and Sen-Sarma, Indian J. Agric. Sci. 26 (1) pp. 27-29.

1958. *Nasutitermes matangensiformis*, Ahmad, Biologia. 4 (2) pp. 147 & 150.

1959. *Nasutitermes matangensis matangensiformis*, Prashid and Sen-Sarma, Indian Coun. Agr. Res. pp. 51-52.

1965. *Nasutitermes matangensiformis,* Ahmad.. Bull. Am. Mus. Nat. Hist. 131 (1) pp. 76-79.

1969. *Nasutitermes matangensis matangensiformis*, Roonwal. Bull. syst. Zool. 1 (2) pp. 41-43.

1981. *Nasutitermes matangensiformis*, Thapa. Sabah Forest Record. 12. pp. 309-312.

1992. *Nasutitermes matangensis matangensiformis*, Thakur & Thakur. Treubia, 30 (3). pp. 193-296.

1992. *Nasutitermes matangensiformis*, Tho. Malayan Forest Records. 36. p. 150.

Havilanditermes

Havilanditermes was described as a subgenus by Light (1930) and Snyder (1949) gave it generic status. Neither these authors nor any subsequent ones (Ahmad, 1965, Thapa, 1981, Tho, 1982, 1992) have given any reason why it should be a separate genus. The only characters which these authors used to distinguish *Havilanditermes* from *Nasutitermes* are size and the presence of a minute tooth below the apical process of the soldier mandibles. Some *Nasutitermes* species (i.e. *N. longinasus* (Holmgren)) have a size range which encompasses that of *Havilanditermes.* As discussed above, the apical processes of the soldiers of Nasutitermitinae are not consistent characters. I have examined soldier and worker material from the BMNH collection and the shape of the soldier head capsule of

Havilanditermes is very similar to that of many *Nasutitermes* species. *Havilanditermes* worker mandibles are very similar to those of *Nasutitermes matangensis*. As neither size, the apical processes of the soldier mandibles, nor the worker mandibles can be consistently used to separate *Havilanditermes* from *Nasutitermes*, I consider that *Havilanditermes* is not a valid genus, and that it is a junior synonym of *Nasutitermes*. Therefore *H. atripennis* (Haviland) and *H. proatripennis* Ahmad are now *Nasutitermes* species.

Identification

The problem of *Nasutitermes* and *Bulbitermes* Emerson.

Nasutitermes and *Bulbitermes* are poorly defined genera. Both genera are defined negatively, i.e. *Bulbitermes* is the wood-feeding South East Asian nasute genus that has constrictions behind the antennal sockets on the soldiers and that is not *Longipeditermes* Holmgren, *Lacessititermes* Holmgren, *Hospitalitermes* Holmgren or *Ceylonitermes*. This makes *Bulbitermes* hard to define as a single coherent entity, without reference to other genera. The many new species which have been discovered in the past few years (e.g. Eggleton *et al.* 1997, Gathorne-Hardy *et al.* submitted) push even the above definition to its limits (i.e. *B.* sp. 1, where the constriction behind the antennae is hardly visible, see key for an illustration). The situation is similar in the case of *Nasutitermes*. It is probable that both *Bulbitermes* and *Nasutitermes* are paraphyletic genera. A full taxonomic revision is needed to resolve the difficulties in defining these genera.

The importance of examining worker characters

From my examination of paratypes in the NHM collection and material collected in Sabah (East Malaysia), Jambi (Central Sumatra) and the Leuser Ecosystem it is clear that it is essential to examine the worker characters of the soil-feeding *Nasutitermes* group in order to identify material to genus. Soldiers of two different genera can appear identical. For example, Ahmad (1968) described *Oriensubulitermes borneensis* from soldiers only. When I examined the worker mandibles of paratype material of *O. borneensis* (which were collected from the same site as the holotype, and identified by Ahmad) I found it to be of the genus *Subulioiditermes*. Presumably the holotype is from the same colony and is also *Subulioiditermes*. *O. borneensis* is therefore *S. borneensis*.

Tho's (1982, 1992) and Collins' (1984) specimens identified as *O. borneensis* have been misidentified. I have examined Collins' collection (in the BMNH) and they are actually *O. inanis* Emerson. From Tho's drawings and measurements, the termites he identified as *O. borneensis* are almost certainly *O. inanis* too.

On the need for a new key to the South East Asian genera of Nasutitermitinae

The most recent key to the Nasutitermitinae in South East Asia (Tho, 1992) needs to be updated, as several characters traditionally used to separate genera have been found to be quite variable. For example, the lack of apical processes on the soldier mandibles of the soil-feeding *Nasutitermes*-group has traditionally been used to split it from other Nasutitermitinae. However, apical processes are very variable (Tho, 1992, Hoare & Jones, 1998, personal observations). Some termites within the soil feeding *Nasutitermes*-group (i.e. some *Malaysiotermes* species) have apical processes and some of the wood-feeding Nasutitermitinae do not have them (e.g.

Nasutitermes longinasus). In other species (i.e. *Leucopitermes leucop*s (Holmgren) and *Sabahitermes leuserensis*) some individual soldiers possess apical processes and others do not. The discoveries of new species also means that many of the characters which had been used to differentiate between genera are now less clear.

Both soldier and worker characters are needed for identification of the South East Asian Nasutitermitinae, as the genera are very similar to each other. As one caste is seldom collected without the other I have therefore used a combination of characters from both castes in my key.

Abundance data from transects run in Sumatra, Borneo, Peninsular Malaysia, Thailand and Java (Termite Research Group, unpublished data) give a rough estimate of the relative abundances of the nasute genera of South East Asia. The number of encounters of a genus as a percentage of the total Nasutitermitinae encounters is given. In the key I have put the genera into the following categories: Very rare (<1%), quite rare (1-5%), common (6-10%) and very common (>10%).

The key is to the genera of Nasutitermitinae in Sundaland. Following the generic key is a key to the species of soil-feeding Nasutitermitinae found in Sundaland.

Figure 4.2 Key to the Nasutitermitinae of the Sunda region

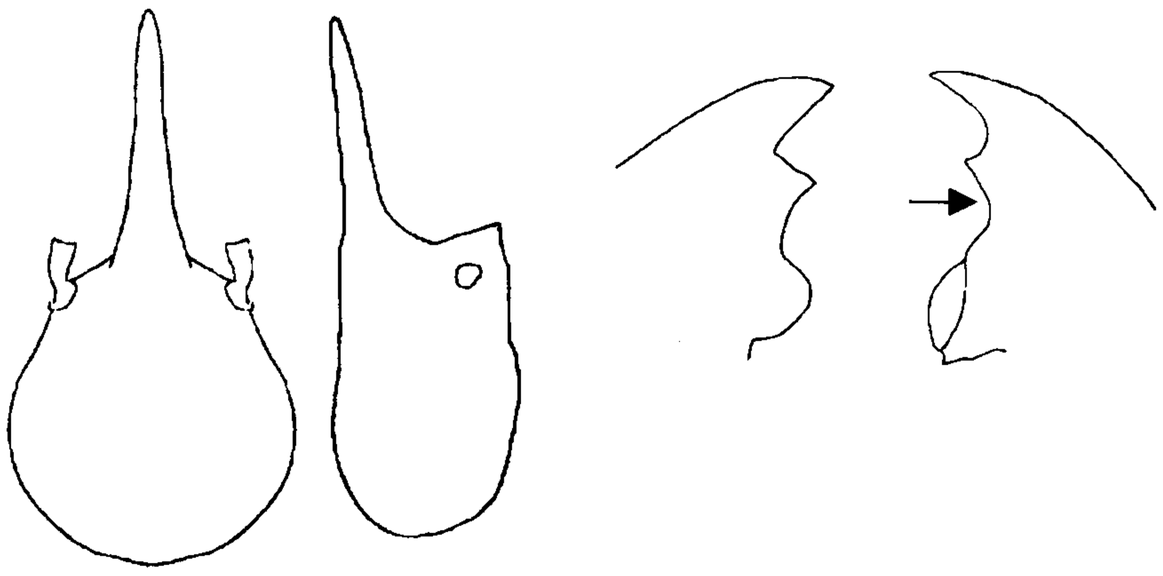
1a: Worker bodies completely unsclerotised, guts clearly visible.....2

1b:Worker bodies sclerotised on dorsal side, guts partly or completely obscured.....8

2a: Apical tooth of worker mandibles longer than first marginal tooth.....3

2b: Apical tooth of worker mandibles shorter or the same length as first marginal tooth.....5

3a: Right worker mandible with second marginal tooth almost completely regressed..... *Oriensubulitermes*

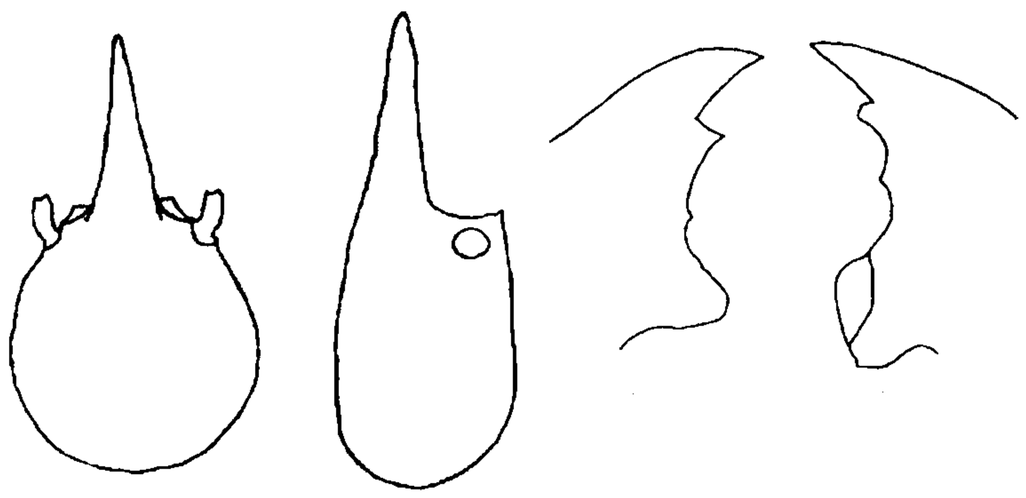


Oriensubulitermes inanis

Oriensubulitermes nests and feeds in soil. The soldier is very similar to *Subulioiditermes*, these two genera can only be separated effectively by using worker mandible characters. Enteric valve with c. 15 small spines per ridge. The spines are larger than those of *Subulioiditermes*. Recorded from Borneo, Sumatra and Peninsular Malaysia.

3b:Right worker mandible with clearly developed second marginal tooth.....4

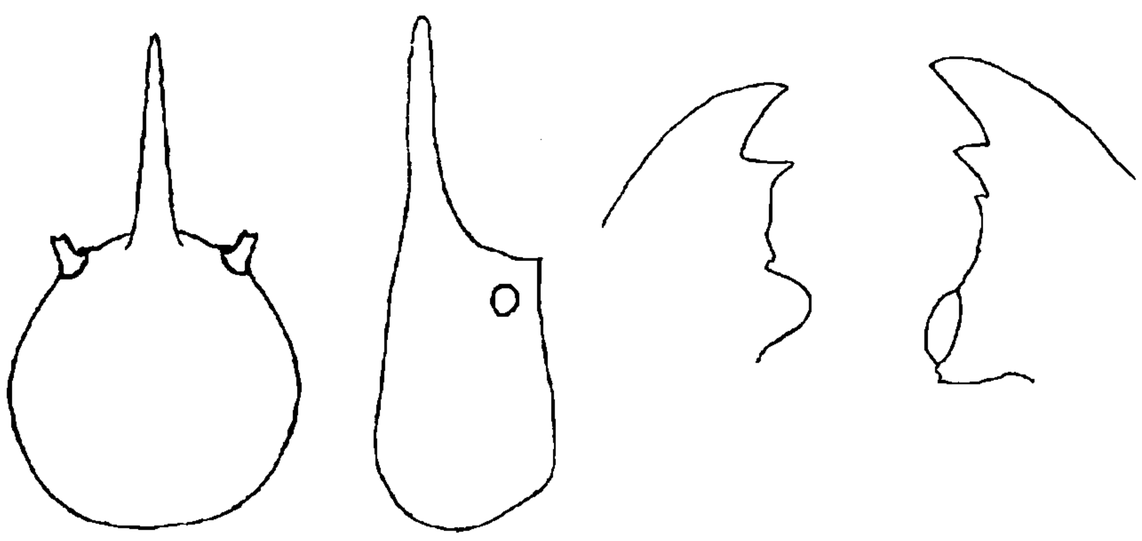
4a: Left mandible index (LMI) = 1 - 1.35..... *Subulioiditermes*.



Subulioiditermes emersoni

Subulioiditermes nests and feeds in soil. The soldier is very similar to *Oriensubulitermes* and these two genera can only be effectively separated by using worker mandible characters. Enteric valve with c. 15 small spines per ridge. The spines are smaller than those of *Oriensubulitermes*. Recorded from Borneo, Sumatra and Peninsular Malaysia.

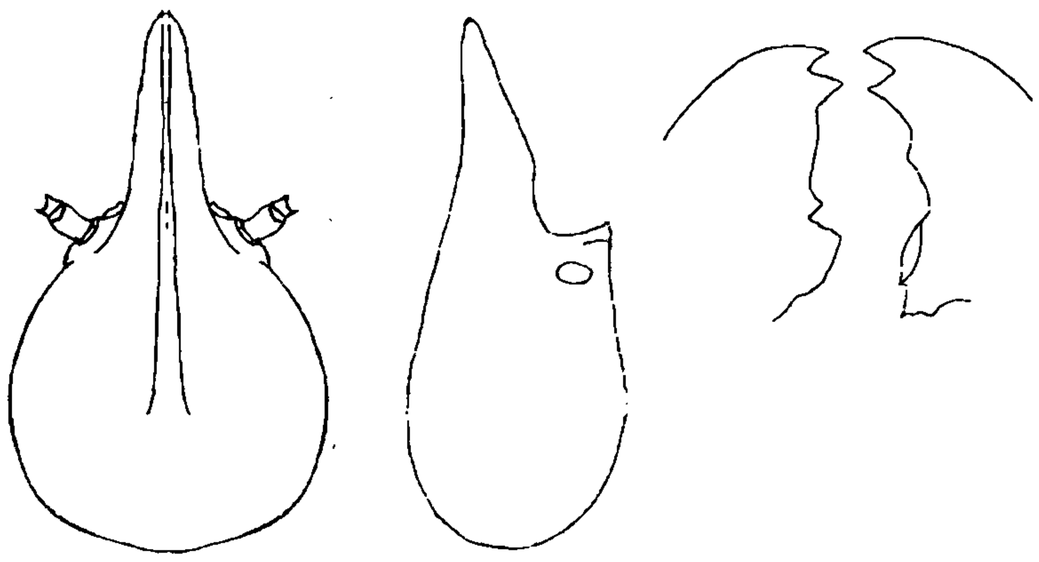
4b: LMI = 0.7-0.8 ..... *Aciculitermes*.



Aciculitermes aciculatus

Aciculitermes nests and feeds in soil. The soldier is very difficult to distinguish from other genera but the LMI is diagnostic. Recorded from Borneo, Sumatra and Peninsular Malaysia.

5a: Soldier nasus thick at base, conical..... *Sabahitermes*

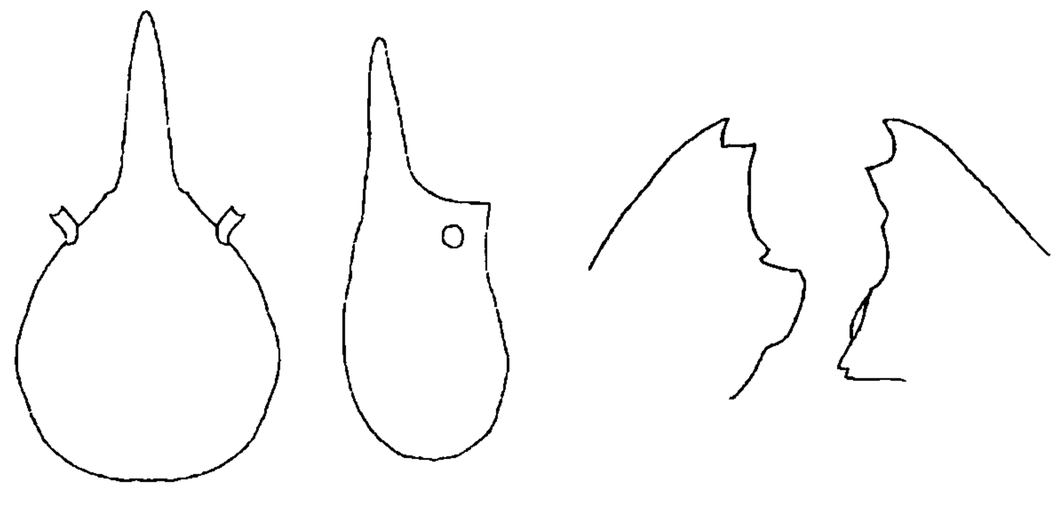


Sabahitermes leuserensis

Sabahitermes nests and feeds in soil. The worker mandibles are very similar to those of *Eleanoritermes* and *Malaysiotermes*. However the enteric valve is very different. In *Sabahitermes* there are c. 30 spines per ridge, while *Malaysiotermes* has only two spines per ridge and *Eleanoritermes* has spines on only three ridges. Recorded from Sumatra, the Malay peninsula and Borneo.

5b: Soldier nasus thin at base, cylindrical. Head bald to moderately hairy.....6

6a: Soldier with eleven antennal segments..... *Eleanoritermes*

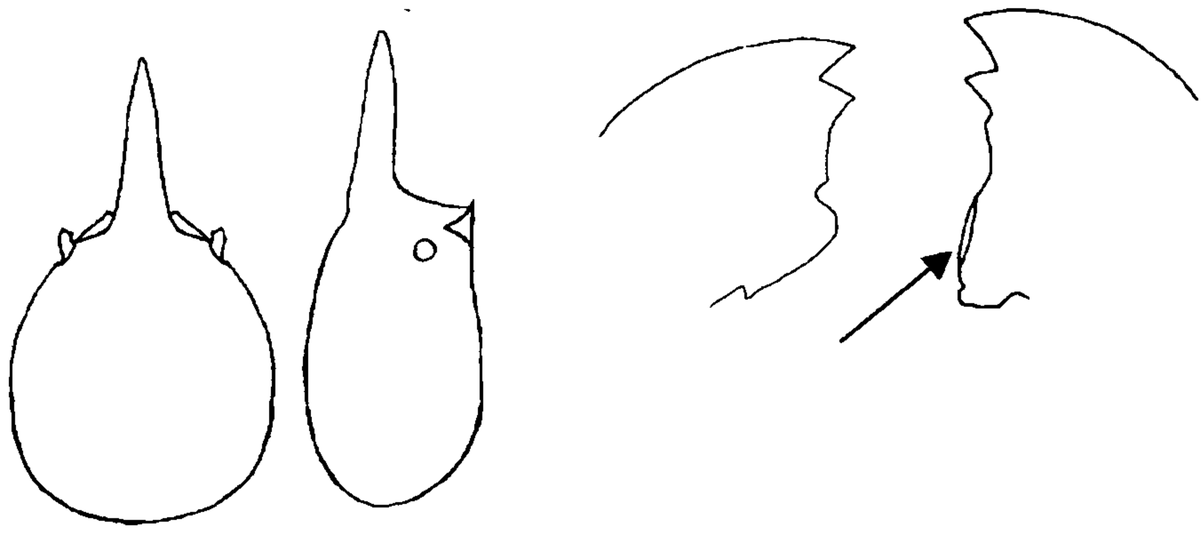


Eleanoritermes borneensis

Eleanoritermes nests and feeds in soil. The soldier head is hairy. The worker mandibles are very similar to those of *Malaysiotermes* and *Sabahiitermes*. The enteric valve has a few spines on three ridges. Recorded from Borneo.

6b: Soldier with more than eleven antennal segments.....7

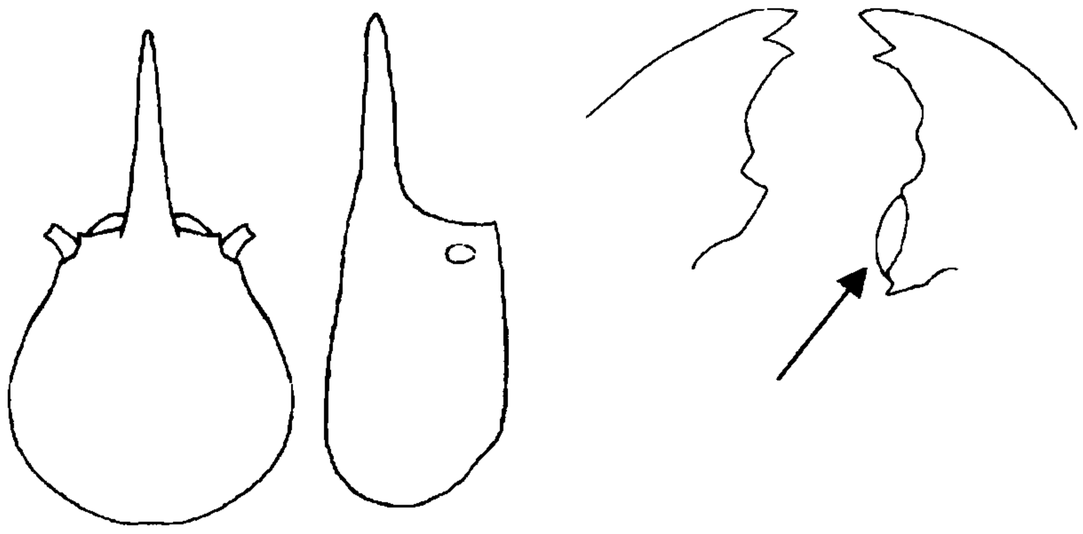
7a: Molar plate of right worker mandible is not concave..... *Leucopitermes*



Leucopitermes leucops

Leucopitermes nests and feeds in soil. The soldier head is more square in shape than that of *Malaysiotermes*.The enteric valve is relatively easy to dissect. It has three ridges each with c. 30 small spines and three ridges with c. 10 smaller spines. This character reliably separates *Leucopitermes* from all other SE Asian Nasutitermitinae. Recorded from Borneo, Sumatra and Peninsular Malaysia.

7b: The molar plate of right worker mandible is concave..... *Malaysiotermes*



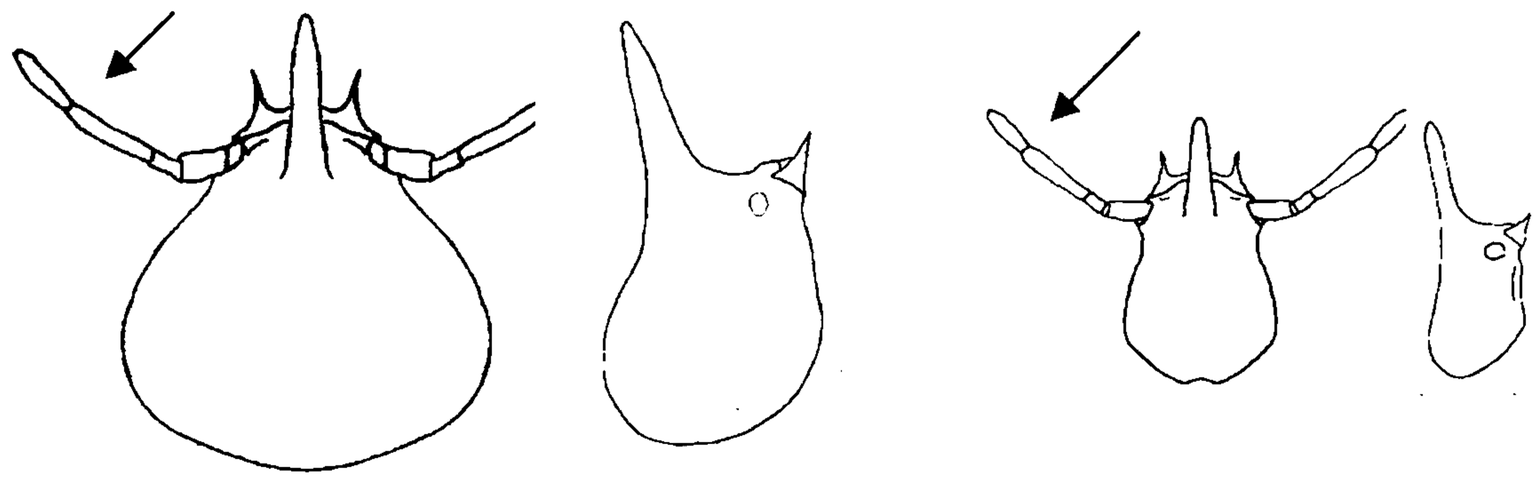
Malaysiotermes malayanus

Malaysiotermes nests and feeds in soil. Soldier heads are bald to moderately hairy. The enteric valve is small, very hard to dissect and has two small spines on each ridge. Common. Recorded from Borneo, Sumatra, Peninsular Malaysia and Java.

8a: Free ranging. Soldiers have long antennal segments (segments three and four at least twice as long as wide), head constricted behind antennae, head and body heavily pigmented and long legs (femur extending beyond or almost beyond the abdomen).....9

8b: Soldiers do not have all of the above characters (though they may have some).....11

9a: Soldiers' third antennal segment twice as long as fourth. Distinct soldier dimorphism. ...*Longipeditermes*



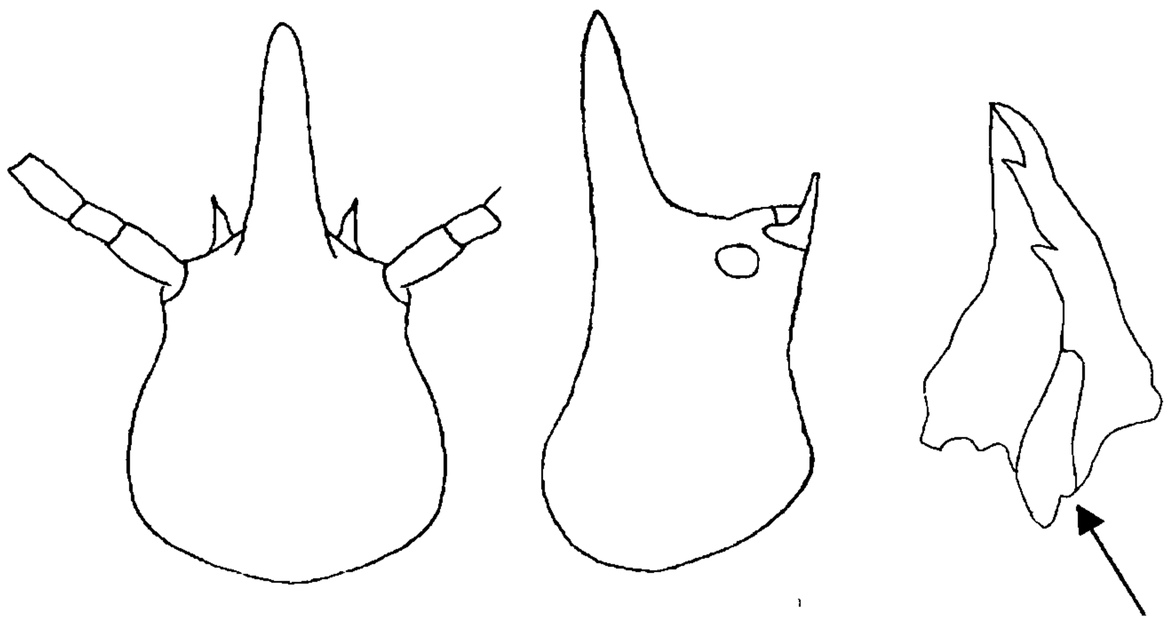
Major soldier Minor soldier

Longipeditermes longipes

Longipeditermes nests in soil and feeds on dead wood and litter. It is usually found in litter, in widespread foraging trails.There are two species in this genus, *L. longipes* and *L. kistneri*. *L.longipes* has white legs and a black body, while *L. kistneri* is brown. Common. Recorded from Borneo, Sumatra and Peninsular Malaysia.

9b: Soldiers' third antennal segment not twice as long as fourth.....10

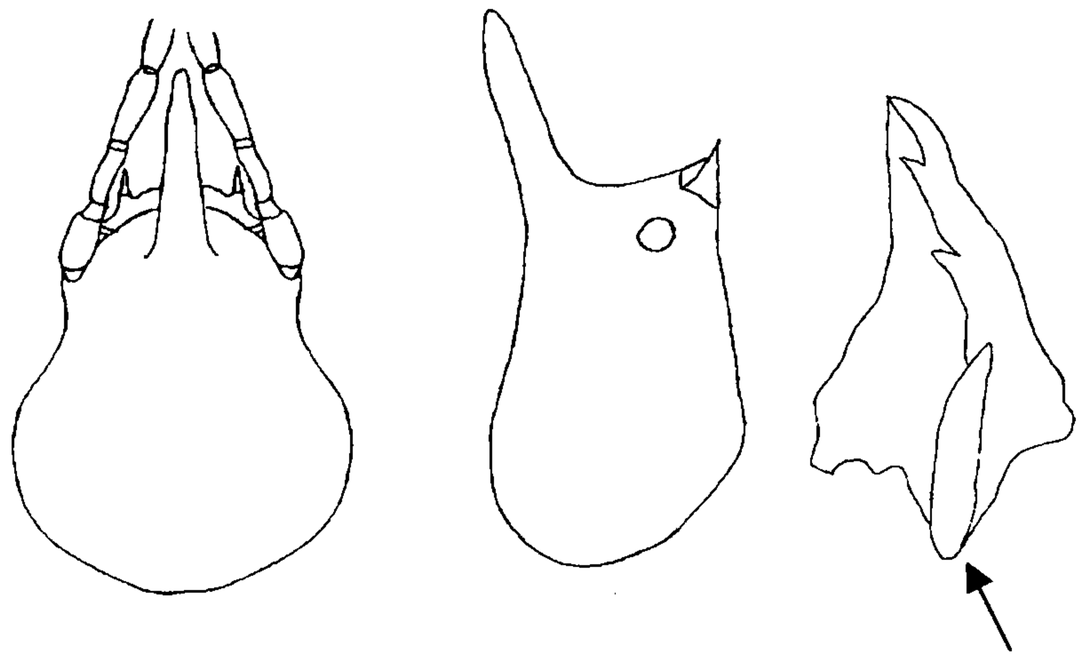
10a: Cockroach notch present on worker mandibles..... *Lacessititermes*



Lacessititermes lacessitus

Lacessititermes nests in round carton, arboreal nests and feeds on litter and dead wood. Has setae on abdominal tergites. Soldier nasus tends to point upwards at a greater angle than that of *Hospitalitermes*. Usually found in a foraging column. Quite rare. Recorded from Borneo, Sumatra, Peninsular Malaysia, Java, Thailand, Vietnam and the Philippines.

10b: No cockroach notch on worker mandibles..... *Hospitalitermes*



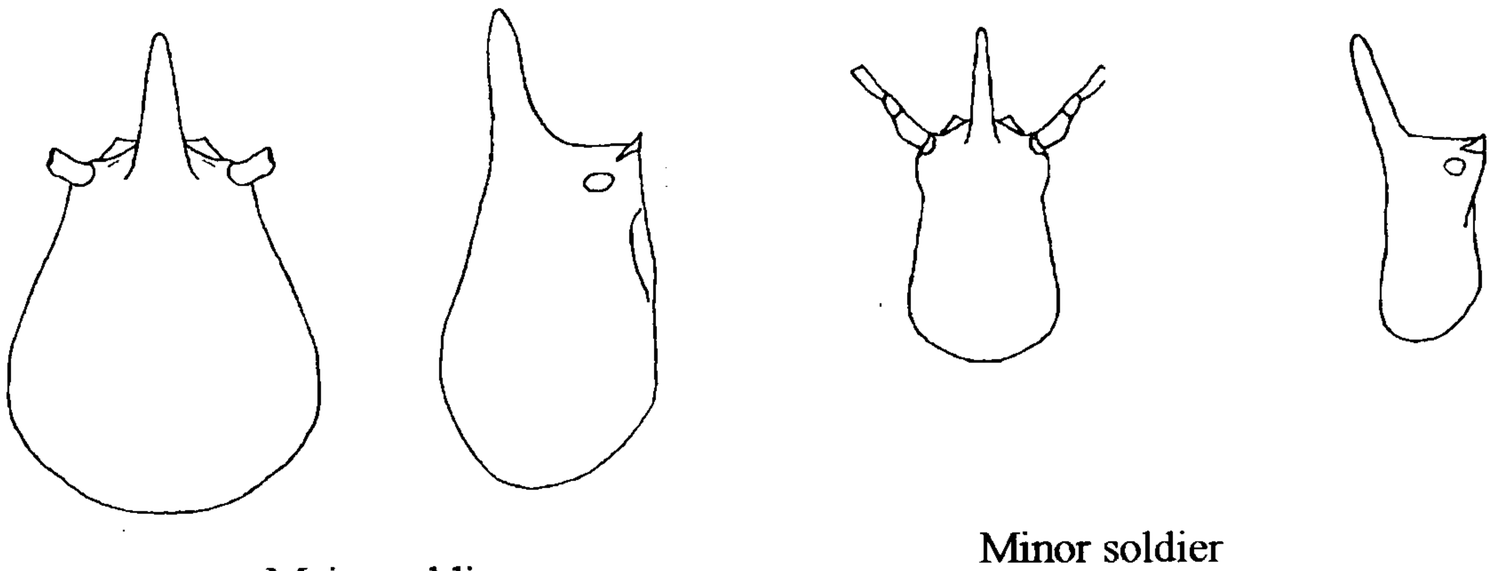
Hospitalitermes hospitalis

Hospitalitermes nests in tree stumps, under roots or up trees and feeds on dead wood, bryophytes and lichens. Usually found in a foraging column, often with workers carrying food balls. No setae on abdominal tergites (except in some species where there are a few on the last three). Quite rare. Recorded from Borneo, Sumatra, Peninsular Malaysia, Java, Thailand, Vietnam, Phillipines, Sulawesi, Cambodia, India, Sri Lanka and New Guinea.

11a: Soldier head constricted behind antennal sockets..... 12

11b: Soldier head not constricted behind antennal sockets..... 13

12a: Dimorphic soldiers. Minor soldier head capsule strongly constricted behind antennae, more or less equal in width in front of and behind the constriction. Very long antennae, more than two times the length of the head. Major soldier head capsule is slightly constricted, much broader behind than in front of than behind the constriction, almost triangular, long antennae, short, cylindrical nasus.....*Ceylonitermes*



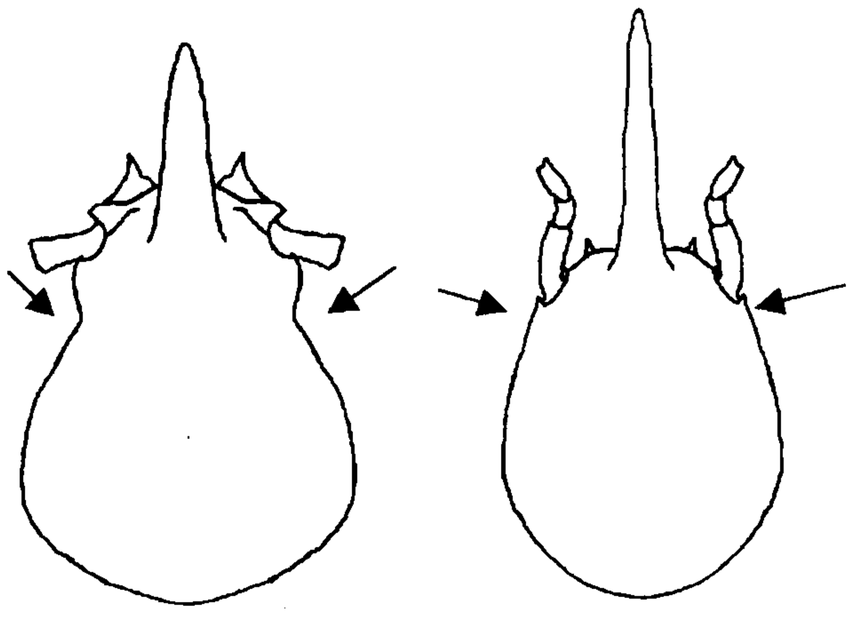
Major soldier

Minor soldier

Ceylonitermes indicola

Ceylonitermes nests among roots in the soil and feeds on dead wood. The minor soldiers are very aggressive and are more commonly collected than the major soldiers. Quite rare. Recorded from Borneo, Sumatra, Peninsular Malaysia, India and Sri Lanka.

12b: Monomorphic soldiers. Head capsule slightly to strongly constricted behind antennal sockets. Deep cockroach notch on worker mandibles.....*Bulbitermes*

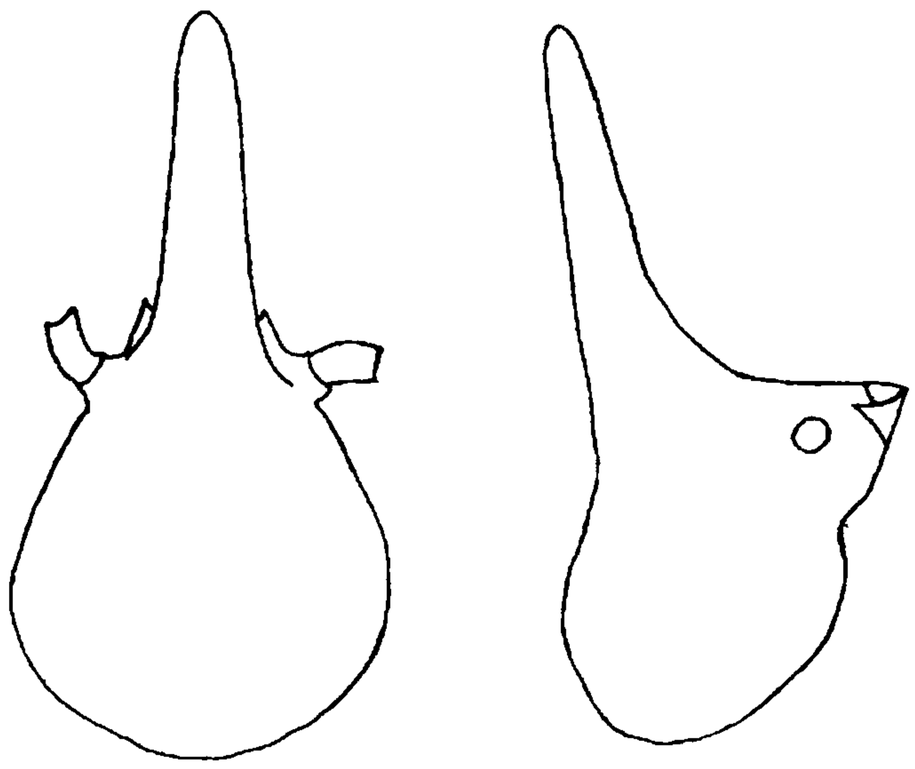


Bulbitermes constrictus

B. sp. 1

Bulbitermes nests in soil, wood or in arboreal carton nests and feeds on dead wood. The constriction of the head capsule behind the antennal segments which characterises this genus varies greatly. Sometimes it is only just apparent (i.e. *B.* sp1, left). This genus needs to be revised for the generic limits are not clear and there are several species which have an uncertain position within *Bulbitermes*. Worker mandibles have a cockroach notch. Very common. Recorded from Borneo, Sumatra, Peninsular Malaysia, Java, and Thailand.

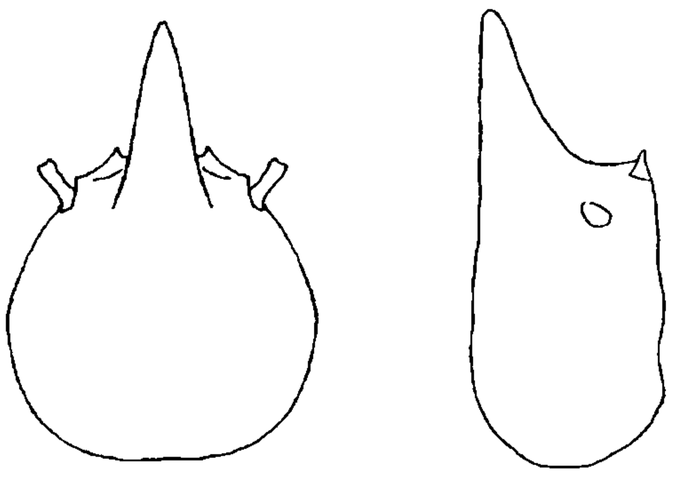
13a: Nasus longer than head capsule. Soldiers and workers generally have thick, stout setae on body. ..... *Hirtitermes*



Hirtitermes hirtiventris

Hirtitermes nests in or under rotten wood and feeds on dead wood. Thick setae on the soldier abdomen characterise most species in this genus. *H. brabazoni*, from Sulawesi has no setae on the tergites but they are present on the sternites. Quite rare. Recorded from Borneo, Sumatra, Sulawesi and Peninsular Malaysia.

13b: Soldiers and workers not thickly covered by setae..... *Nasutitermes*



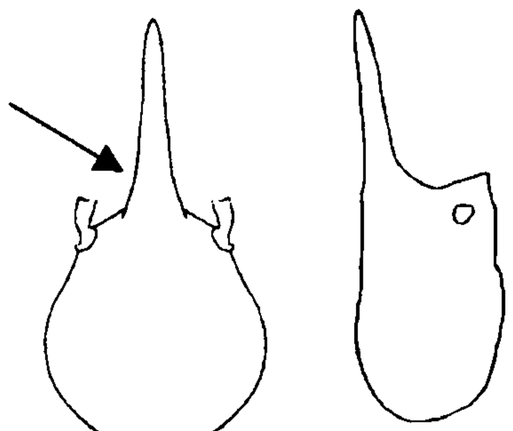
Nasutitermes matangensis

Nasutitermes nests in dead wood, soil or in arboreal carton nests and feeds on dead wood. Cockroach notch absent or appears as only a slight indentation. The generic limits of *Nasutitermes* are not clear and it appears to be paraphyletic. This genus needs to be revised. Very Common. Recorded throughout South-East Asia.

Key to species of soil-feeding Nasutitermitinae from the Sunda region

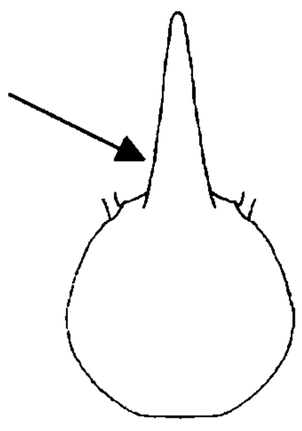
***Oriensubulitermes* Emerson**

1a. Thin cylindrical nasus. Head may be round or slightly constricted behind antennal segments.....
O. inanis



Size varies considerably.

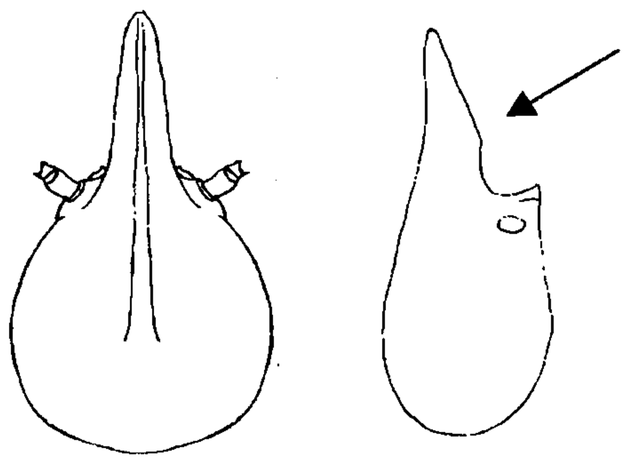
2a. Broad, conical nasus. Head is broadly oval.....*O. kemneri*



O. kemneri is much rarer than *O. inanis*, and has been only found in northern Borneo and northern Sumatra.

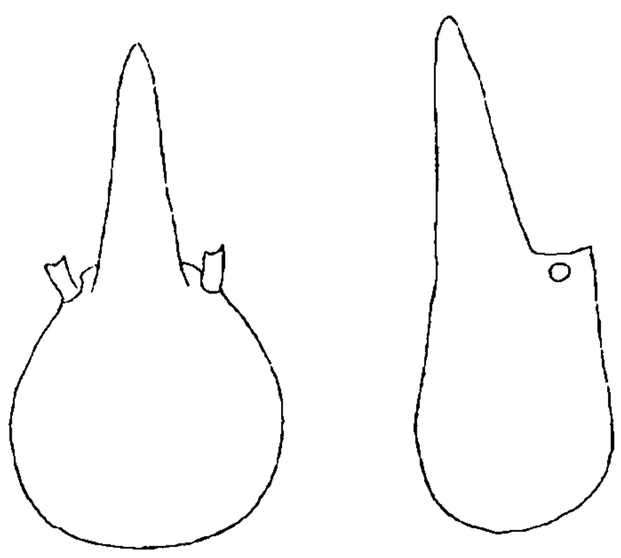
***Sabahitermes* Thapa**

1a. Nasus obviously upturned, thickly hairy, rostrum: head ratio= 0.7.....*S. leuserensis*



Found only in northern Sumatra

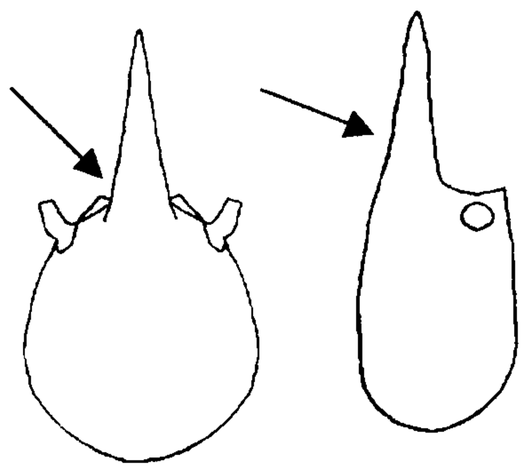
1b. Nasus not so upturned, not thickly hairy, rostrum: head ratio= 0.9.....*S. malakuni*



Found only in northern Borneo

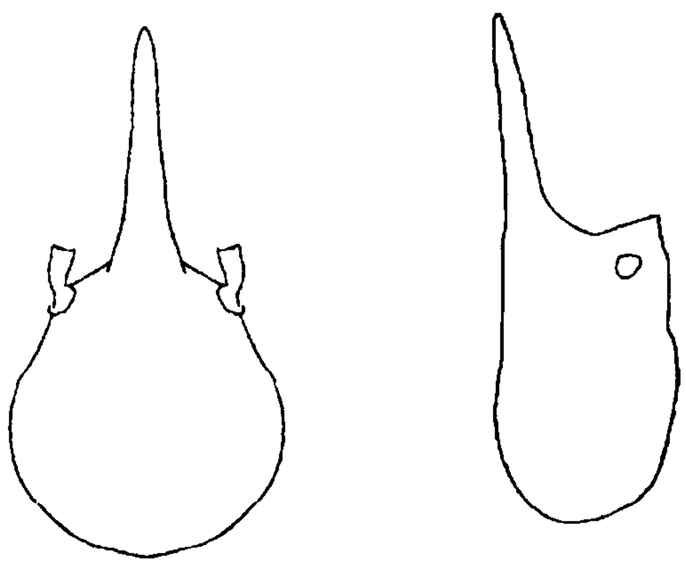
***Subulioiditermes* Ahmad**

1a. Broad, conical and downward-pointed nasus.....*S. emersoni*



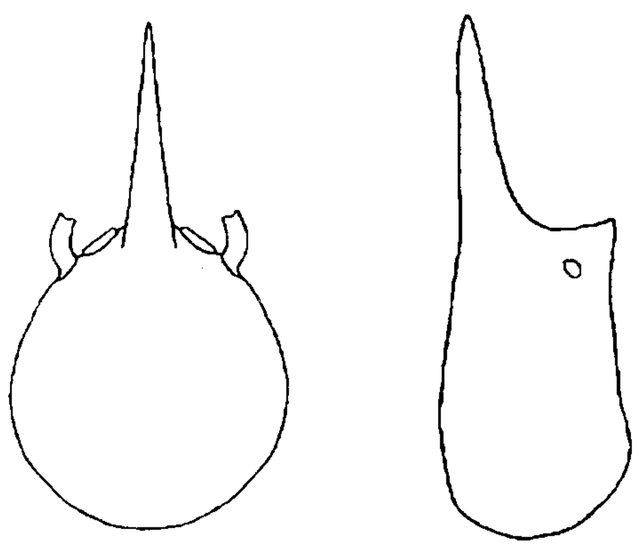
This is a very rare species, and has only been collected twice; from Sarawak and Sabah.

1b. Thin, cylindrical nasus. Not downward-pointing.....2
2a. Head length with rostrum longer than 1.66 mm.....*S. borneensis*



Very rare. It has only been collected once, from Sarawak

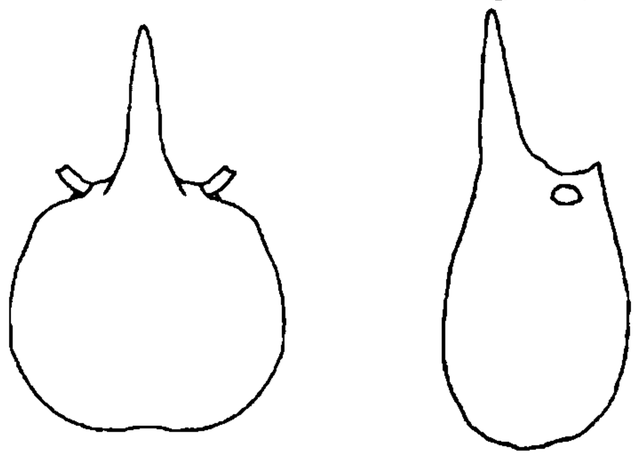
2b. Head length with rostrum shorter than 1.4 mm.....*S. subulioides*



This species is more common than the other two, and has been collected from Sumatra, Borneo and Peninsula Malaysia.

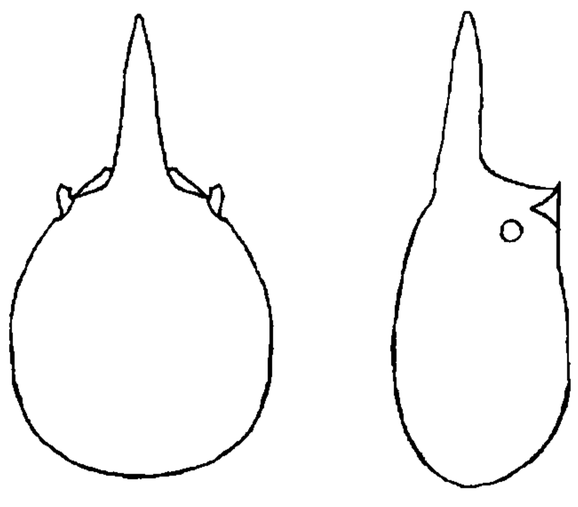
***Leucopitermes* Emerson**

1a. Head capsule almost rectangular, head very large in proportion to body.....*L. thoii*



This species is rare and has been found in Sumatra and the Malay Peninsula

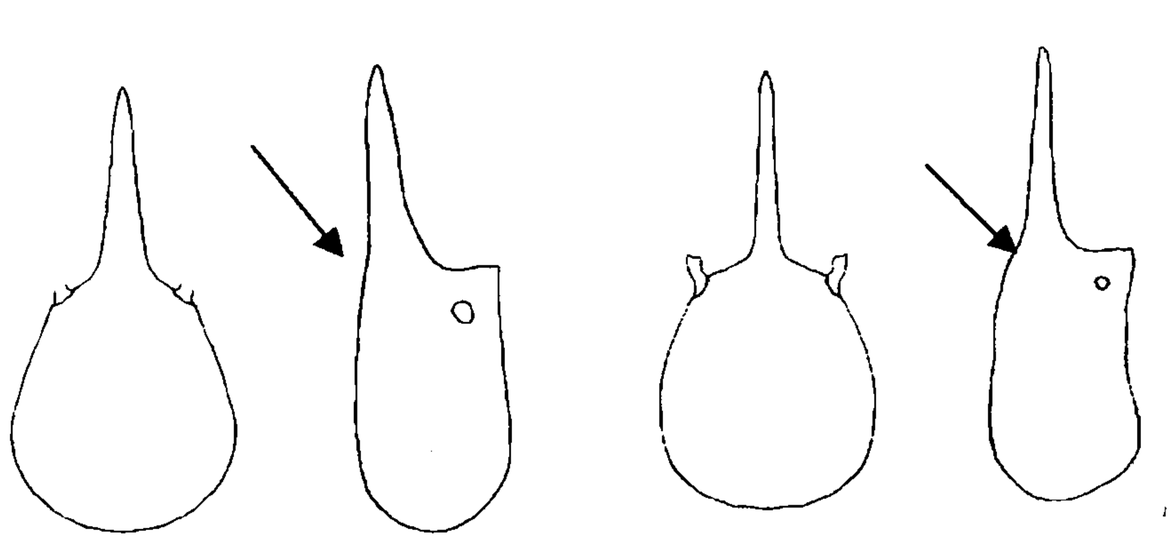
1b. Head capsule rounded,not large in proportion to body.....*L. leucops*



This species is quite common and has been found in Borneo, Sumatra and Peninsula Malaysia.

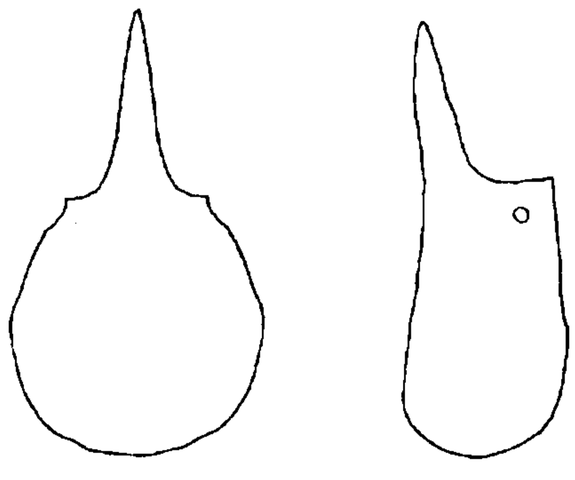
***Malaysiotermes* Ahmad**

1a. Head hairy (this is best seen against a dark background, under high magnification)....*M. spinocephalus*



The degree at which the hump at the base of the rostrum is expressed varies considerably. The width of the rostrum varies too. These figures show some of the variation in this species.

1b. Head not hairy.....*M. holmgreni*



4.3 DESCRIPTIONS

FAMILY TERMITIDAE LIGHT, 1921

SUBFAMILY NASUTITERMITINAE HARE, 1937

Sabahitermes leuserensis new species

Etymology

leuserensis refers to the Leuser Ecosystem in Sumatra where this species was discovered.

Holotype-One specimen soldier caste. From soil, Ketambe field station, Aceh Tenggara, Indonesia. coll. Sugesti, Sept. 1998. Deposited in Bogor Zoological Museum, Bogor, Indonesia.

Paratypes-Soldiers, workers and one specimen imago. From soil, Ketambe field station, Aceh Tenggara, Indonesia. coll. Sugesti, Sept. 1998 . Deposited in Bogor Zoological Museum, Bogor, Indonesia.

Soldiers, workers. Leuser Ecosystem, northern Sumatra, Indonesia. coll. Hasballah, Sugesti, Syaukani, Gathorne-Hardy, Sept-Oct 1998. Deposited in Syiah Kuala University, Darussalam, Banda Aceh, Indonesia.

Soldiers, workers. Leuser Ecosystem, northern Sumatra, Indonesia. coll. Hasballah, Sugesti, Syaukani, Gathorne-Hardy, Sept-Oct 1998. Deposited in Natural History Museum, London, U.K.

Habitat-Undisturbed tropical rainforest, up to 1250 m. Found in soil, in amorphous nests. Feeds on decomposed, slightly humified plant material.

Measurements- see table 2

Imago

Head capsule dark reddish brown, vertex colour uniform, frons uniform colour apart from frontal marks of muscle attachments. Genae strong brown, postclypeus and labrum brownish yellow. Antennae yellowish brown. Fontanelle pale yellow, pronotum dark brown, mesonotum very pale brown, metanotum very pale brown. Legs yellow. Wing membrane yellow, main wing venation dark reddish brown. Abdominal tergites and sternites dark brown.

Head capsule (disregarding compound eyes) parallel-sided, rounded in front, posterior margin evenly rounded but less than semicircular. Epicranial suture absent. Fontanelle broadly circular, equal in size to ocellus, slightly depressed on side view, centred in front of line joining posterior margins of compound eyes. Ocelli present. Frons flat or at the most weakly indented in front of the fontanelle. Posterior margin of postclypeus arcuate, clearly inflated in contour, labrum weakly curved, not inflated in profile. Anterior margin of pronotum is slightly lobed in the middle.

Vertex of pronotum densely pilose, forming a pelt with emergent longer setae. 15 antennal articles.

Fore coxae without prominent spine-like setae. Tibial spurs 2:2:2. Tarsi (viewed from above) four-segmented. Forewing bases are larger than those of the hindwing and the forewing has costal venation fused and a separate unbranched radial sector. Hindwings missing.

Soldier.

Head capsule yellow, antennae Yellow, pronotum very pale brown, legs very pale brown. Head shape in plan view is circular but wider at back. Sides narrow towards rostrum. Has dense setae with thick "moustache" of hairs on ventral side of nasus. Nasus equal to the length of the head capsule behind the antennae, broadly conical. 14 antennal articles. Postmentum is convex and the sides are more or less uniformly concave, with very few setae. Pronotum in plan view indented in middle, outer corners rounded and not extended. In profile, anterior lobe is smaller than the posterior.

Worker.

Head capsule pale yellow, darkest part of antennal flagellum and pronotum are pale yellow, legs are pale yellow, abdominal tergites are transparent. Head is oval with numerous but not dense setae, separated by less than the length of the longest setae. Head capsule setae are robust, slightly darker than the head capsule, mostly short and roughly the same length and randomly scattered. Epicranial suture is present. Fontanelle, compound eyes and ocelli are absent. Postclypeus with posterior margin is indistinct, while its contour is clearly inflated. The labrum contour is (in

profile) weakly curved. Fifteen antennal articles. Pronotum saddle-shaped. Fore coxae conical, without prominent spine-like setae on the anterior surface. Fore tibiae with regular fringe of prominent setae on the ventral surface, extending for less than the apical half. The longest tibial setae are equal in length to the longest tibial spurs. Middle and hind tibiae have a regular fringe of prominent setae on the ventral surface. Tibial spurs: 2:2:2. Tarsi four-segmented.

Left mandible apical tooth is roughly equal in prominence to the first marginal, second marginal tooth is absent, incorporated into the cutting edge between the first and third. Third marginal tooth distinctly protrudes from the cutting edge of the first plus second, the anterior edge is shorter than that of the first and is separated from the molar prominence by a distinct gap. The fourth marginal tooth is indistinct

Right apical tooth is just shorter than that of the first marginal (all measurements follow those of Roonwal, 1970). The first marginal anterior edge is uniform and longer than that of the second. The second marginal tooth is fully developed and separate from the first, the posterior edge of the first marginal tooth is longer than that of the second. Cockroach notch at proximal end of right molar plate is weakly developed and shallowly obtuse. The molar plate ridges are much reduced, and number five.

Crop is normally dilated in front of the abdomen. Proventriculus has a much reduced armature. Mesenteron is without proximal diverticula and overlaps the proctodeum by two-three times the width of the mesenteron, with a sinuate junction to form a mixed segment. The mesenteric part of the mixed segment is external to the loop of the intestine in ventral view and has a single lobe to one side of the first part of the proctodeum (P1). The intestine with the anterior part of the mesenteron is

longer than the mixed segment. The junction of the mesenteron and the P1 starts beneath the nerve cord in ventral view. At its narrowest point the mesenteric part of the mixed segment is less than half the width of the proctodeal part. The mesenteric part of the mixed segment is not inflated distally. The back end of the mixed segment the ventral view of and unopened abdomen is well to the left of the ventral nerve cord. There are four malpighian tubules which are attached in pairs, closely adjacent at the base directly onto the gut wall at the mesenteric-proctodeal interface. They taper from a broad, ribbon-like base. The attachment is visible in ventral view only, well to the left of the nerve cord. P1 is very long, more than eight times its proximal width and is tubular throughout its length. The termination of the P1 at the enteric valve is not distinct from the rest of the segment. The enteric valve enters directly into the third segment of the proctodeum (P3) and is hidden beneath the mesenteron. The enteric valve seating is invaginated into the P3. The armature of the enteric valve is predominantly within the lumen of the valve. The ridges are unsclerotised and retracted into the lumen of the valve. The main armature of the enteric valve ridges is the same for each; with more than 30 small backwardly directed spines on scales. The spines are straight, small and evenly tapered. The membranous wall of the enteric valve between and beyond the ridges is smooth, without spines. The colon within the mesenteric loop in dorsal view of the unopened abdomen forms only one simple loop.

Comparisons

The soldier of *S. leuserensis* is easily distinguished from all *S. malakuni* by the fact that the nasus of *leuserensis* is very obviously upturned, when seen from the

side, and the rostrum: head ratio is 0.7. *S.* malakuni has a rostrum which is not so upturned and the rostrum: head ratio is 0.9.

Table 4.2 Showing the measurements of *S. leuserensis*

S. leuserensis Soldier

Soldiers, 15 specimens from 4 nests	Range (mm)	Mean (mm)	S.D.
Head Length	1.409-1.874	1.705	0.13
Head width	0.641-1.003	0.876	0.107
Head length to base of rostrum	0.787-1.159	1.017	0.1
Rostrum length	0.614-0.786	0.688	0.047
Rostrum: head ratio	0.564-0.79	0.681	0.062
Head height	0.566-0.844	0.749	0.093
Height pronotum	0.122-0.186	0.161	0.022
Width pronotum	0.355-0.507	0.452	0.044
Width of base of rostrum	0.228-0.303	0.278	0.022
Hind tibia length	1.113-1.146	1.08	0.044

S. leuserensis Workers

Workers. Ten specimens from 4 nests	Range (mm)	Mean (mm)	S.D.
Right mandible, Apical tooth to 1st marginal	0.048-0.069	0.06	0.00728
Right mandible, Apical tooth to 2nd marginal	0.141-0.184	0.168	0.016
Right mandible 1st to 2nd marginal	0.097-0.126	0.112	0.0094
Right mandible index	0.452-0.6	0.532	0.0425
Left mandible, apical tooth to 1st marginal	0.049-0.062	0.056	0.0048
Left mandible, apical tooth to 2nd marginal	0.174-0.221	0.2038	0.0197
Left mandible, 1st to 2nd marginal	0.132-0.173	0.156	0.0144
Left mandible index	0.329-0.394	0.361	0.017
Head length	0.586-0.714	0.653	0.0399
Head width	0.767-0.886	0.835	0.0332
Fore tibia	0.639-0.813	0.712	0.053
Fore tibia width	0.067-0.102	0.077	0.013
Fore tibia index	7.971-9.973	9.375	0.751
Hind tibia	0.862-1.115	0.953	0.07

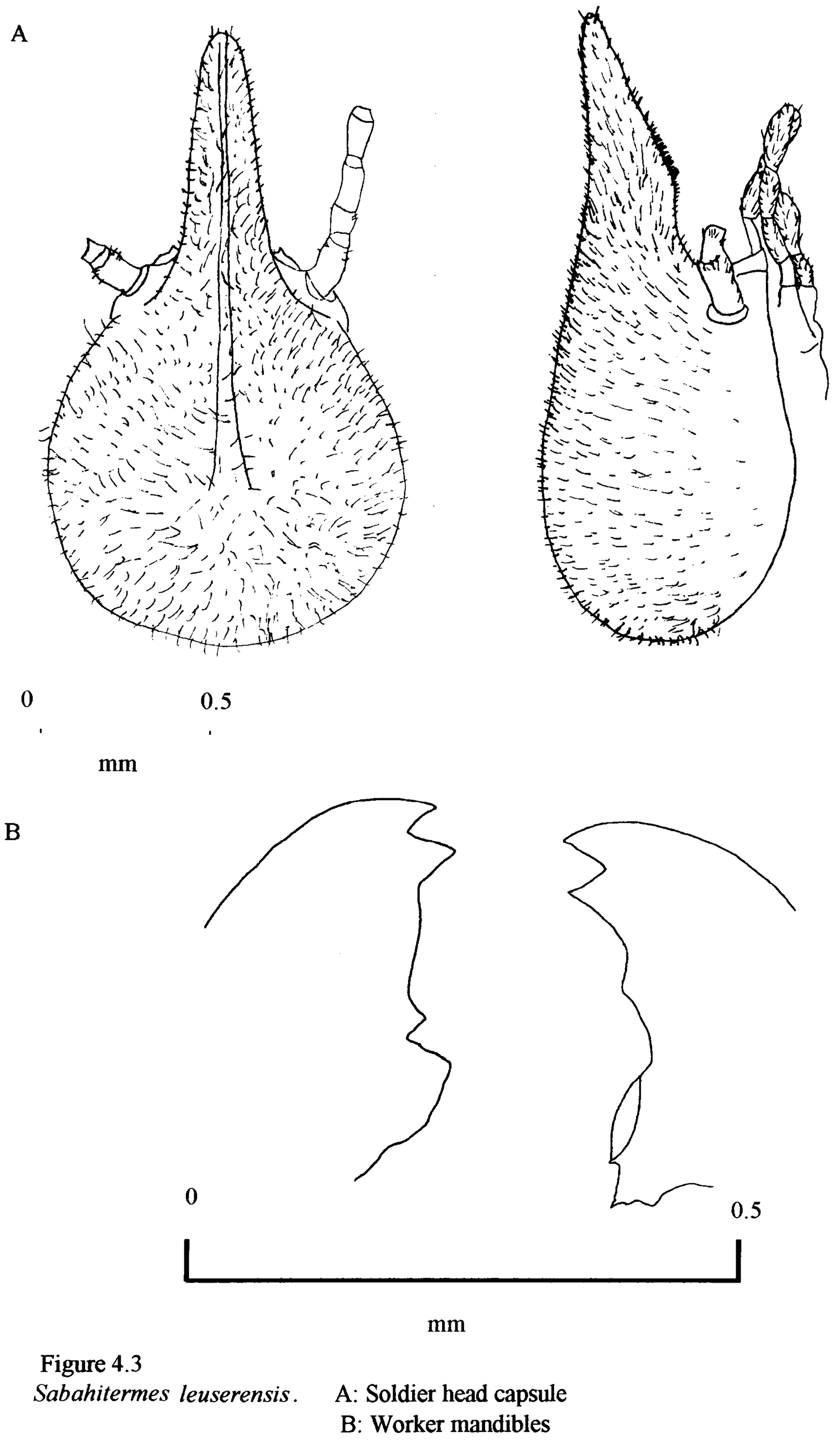


Figure 4.3
Sabahitermes leuserensis. A: Soldier head capsule
B: Worker mandibles

Ceylonitermes indicola

Worker and minor soldier are described in Thakur (1976) pp 15-17.

Major soldiers deposited in Bogor Zoological Museum, Bogor, Indonesia; Syiah Kuala University, Darussalam, Banda Aceh, Indonesia and the Natural History Museum, London, England.

Measurements-

Table 4.3. Showing the measurements of *C. indicola* major soldier

Ceylonitermes indicola Major soldier

Ceylonitermes indicola (Major soldier) 14 specimens from two sites	Range (mm)	Mean (mm)	S.D.
Head Length	1.711-1.968	1.817	0.092
Head width	1.05-1.384	1.21	0.096
Head length to base of rostrum	1.19-1.431	1.307	0.068
Rostrum length	0.397-0.63	0.51	0.06
Rostrum: head ratio	0.302-0.513	0.391	0.051
Head height	0.865-1.061	0.962	0.093
Height pronotum	0.178-0.216	0.194	0.012
Width pronotum	0.462-0.563	0.504	0.032
Hind tibia length	1.014-1.17	1.103	0.045

Major Soldier.

Head capsule, antennae and pronotum colour varies from reddish yellow to yellowish red. Legs yellow to reddish yellow. Head capsule in plan view has straight sides, which converge onto the front. Setae are very sparse on the head capsule, which is smooth and shiny. Nasus is shorter than head capsule behind antennae and is parallel sided for most of its length. The tip of the nasus has four large setae around the rim. Thirteen antennal articles. Postmentum is weakly and evenly convex, with sides more or less uniformly concave and at the most, one or two setae. Pronotum in plan view is broadly lobed in the middle, with the front margin entire. In profile view the anterior lobe is smaller than the posterior.

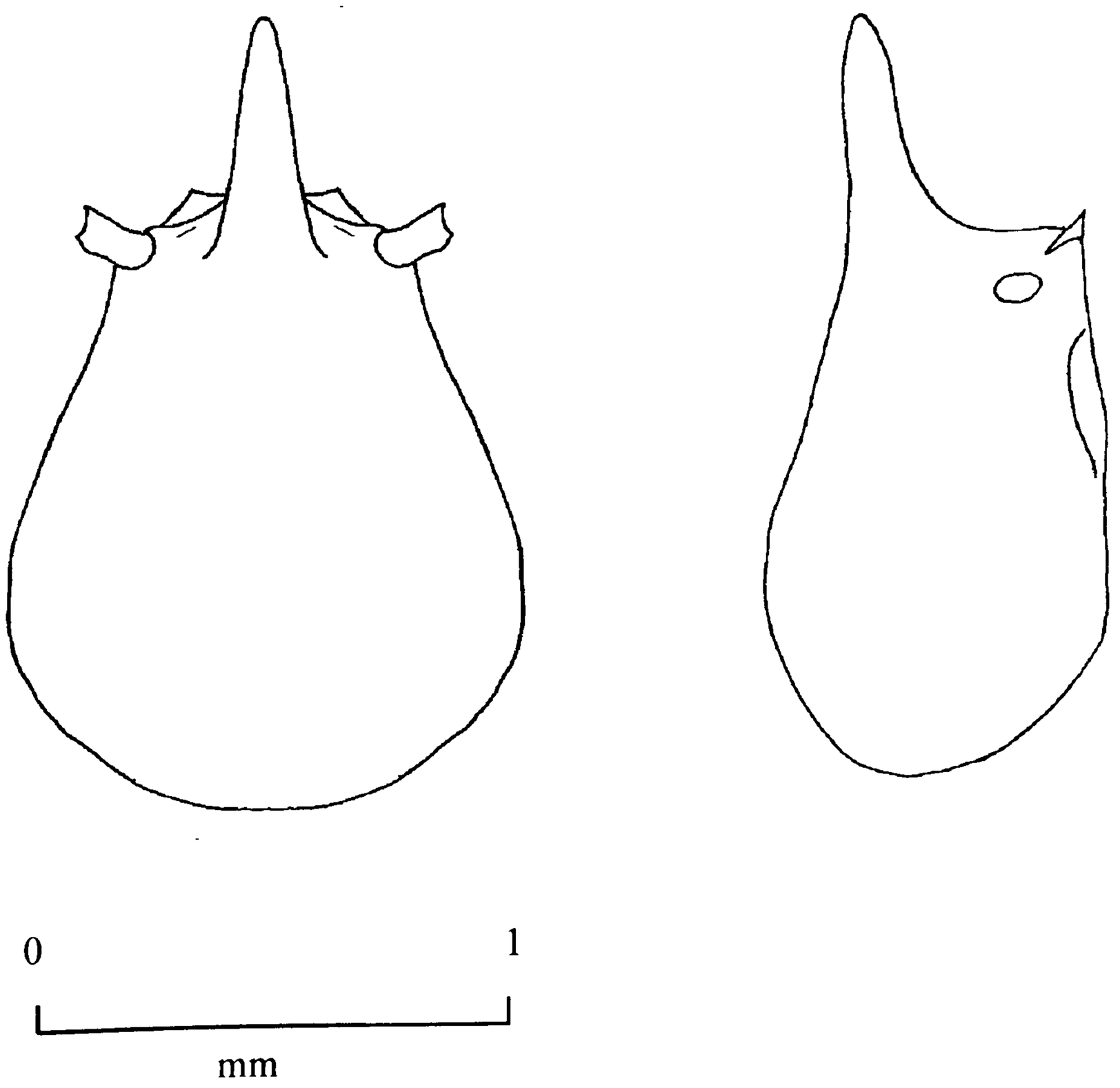


Figure 4.4: *Ceylonitermes indicola* Thakur. Major

Hirtitermes Holmgren

Hirtitermes brabazoni new species

Etymology

This species is named after Geoffrey William Brabazon, who was killed on 23 November, 1998.

Holotype. One specimen soldier caste Coll. R.D. Buxton and N.M. Collins, 1985. Dumoga-Bone National Park, North Sulawesi, Indonesia. Deposited in Bogor Zoological Museum, Bogor, Indonesia.

Paratypes. Soldiers and workers. Coll. R.D. Buxton and N.M. Collins, 1985. Dumoga-Bone National Park, North Sulawesi, Indonesia. Deposited in Bogor Zoological Museum, Bogor, Indonesia.

Paratypes. Soldiers and workers. Coll. R.D. Buxton and N.M. Collins, 1985. Dumoga-Bone National Park, North Sulawesi, Indonesia. Deposited in British Museum (Natural History), London, England.

Habitat- Lowland rainforest. Feeds on wood. Sulawesi and Borneo.

Measurements- See table 4.4

Soldier.

Head capsule reddish yellow, rostrum becomes progressively darker towards tip, where it is dark reddish brown. Antennae are reddish yellow and the legs are yellow. Head shape in plan view circular but wider at the back, with sides narrow towards the rostrum. There is generally no hair (sometimes one or two hairs are present) on the head and the head capsule is smooth and shiny. There are four large setae in a regular rim around the fontanelle. The nasus is broadly conical with more or less straight sides in plan view. The tip of the nasus is sharply tapered towards the small fontanelle. There are fourteen antennal segments, though the third segment is sometimes incompletely or not at all divided. The pronotum in plan view has a front margin which is broadly lobed in the middle and entire. The outer corners are rounded and significantly extended. The anterior lobe is smaller than the posterior.

Table 4.4 *Hirtitermes brabazoni* Soldier

Soldiers, 17 specimens from 4 nests	Range (mm)	Mean (mm)	S.D.
Head Length	2.07-2.56	2.35	0.16
Head width	0.999-1.46	1.25	0.13
Head length to base of rostrum	0.94-1.36	1.176	0.14
Rostrum length	1.02-1.37	1.17	0.097
Rostrum: head ratio	0.79-1.29	1.01	0.15
Head height	0.75-1.03	0.9	0.087
Height pronotum	0.19-0.32	0.28	0.034
Width pronotum	0.49-0.73	0.62	0.066
Hind tibia length	1.5-1.9	1.66	0.11

Worker.

Dimorphic. Major worker with brown head capsule and pronotum, minor worker head capsule yellow, pronotum hyaline. Major worker antennae are yellow, minor worker has hyaline antennae. Legs of major worker are yellow while the legs of the minor worker are hyaline, as are the minor worker's abdominal tergites. Major worker's abdominal tergites are dark brown. Minor workers are less sclerotised and the head is paler than the major workers. Head capsule is oval. Only one or two setae are present. There are no visible compound eyes or ocelli. There are fifteen antennal articles. Left mandible apical tooth is roughly equal in prominence to the first marginal. The second marginal tooth is absent, it is fully incorporated into the cutting edge between the first and the third. The third marginal distinctly protrudes from the cutting edge of the first plus second marginals, is separated from the molar prominence by a distinct gap and the anterior edge is shorter than that of the first marginal. The right mandible apical tooth is just shorter than that of the first marginal. The first marginal has a uniform leading edge, this and the posterior edge are longer than those of the second. The second marginal is fully developed and separate from the first and the posterior margin is more or less strait. The notch (cockroach notch) at the proximal end of the molar plate is moderately developed. The molar plate ridges are prominent and number eight.

The worker gut structure is similar to other wood-feeding South East Asian Nasutitermitinae.

Table 4.5 showing the worker measurements of *H. brabazoni*

Major Workers. Eight specimens from 4 nests	Range (mm)	Mean (mm)	S.D.
Right mandible, Apical tooth to 1st marginal	0.075-0.12	0.98	0.016
Right mandible, Apical tooth to 2nd marginal	0.18-0.24	0.21	0.024
Right mandible 1st to 2nd marginal	0.1-0.13	0.12	0.0087
Right mandible index	0.66-0.93	0.84	0.093
Left mandible, apical tooth to 1st marginal	0.064-0.12	0.09	0.017
Left mandible, apical tooth to 3rd marginal	0.22-0.32	0.28	0.032
Left mandible, 1st to 3rd marginal	0.18-0.26	0.21	0.026
Left mandible index	0.29-0.53	0.43	0.074
Head length	1.06-1.4	1.28	0.15
Head width	1.29-1.66	1.51	0.14
Minor Workers. Eight specimens from 4 nests	**Range (mm)**	**Mean (mm)**	**S.D.**
Right mandible, Apical tooth to 1st marginal	0.062-0.073	0.068	0.0045
Right mandible, Apical tooth to 2nd marginal	0.14-0.16	0.15	0.0056
Right mandible 1st to 2nd marginal	0.075-0.091	0.083	0.0051
Right mandible index	0.72-0.91	0.82	0.071
Left mandible, apical tooth to 1st marginal	0.058-0.069	0.062	0.0032
Left mandible, apical tooth to 3rd marginal	0.2-0.22	0.2	0.0073
Left mandible, 1st to 3rd marginal	0.14-0.15	0.15	0.0045
Left mandible index	0.38-0.48	0.42	0.026
Head length	0.82-0.9	0.87	0.024
Head width	0.93-1.19	1.07	0.076

Comparisons

Hirtitermes can be distinguished from other genera by the shape of the soldier head capsule in side view (long nasus, pointing upwards, see fig and key).

Unlike the other two species of *Hirtitermes, H. brabazoni* has no setae on the dorsal part of the body and only short setae on the sternites.

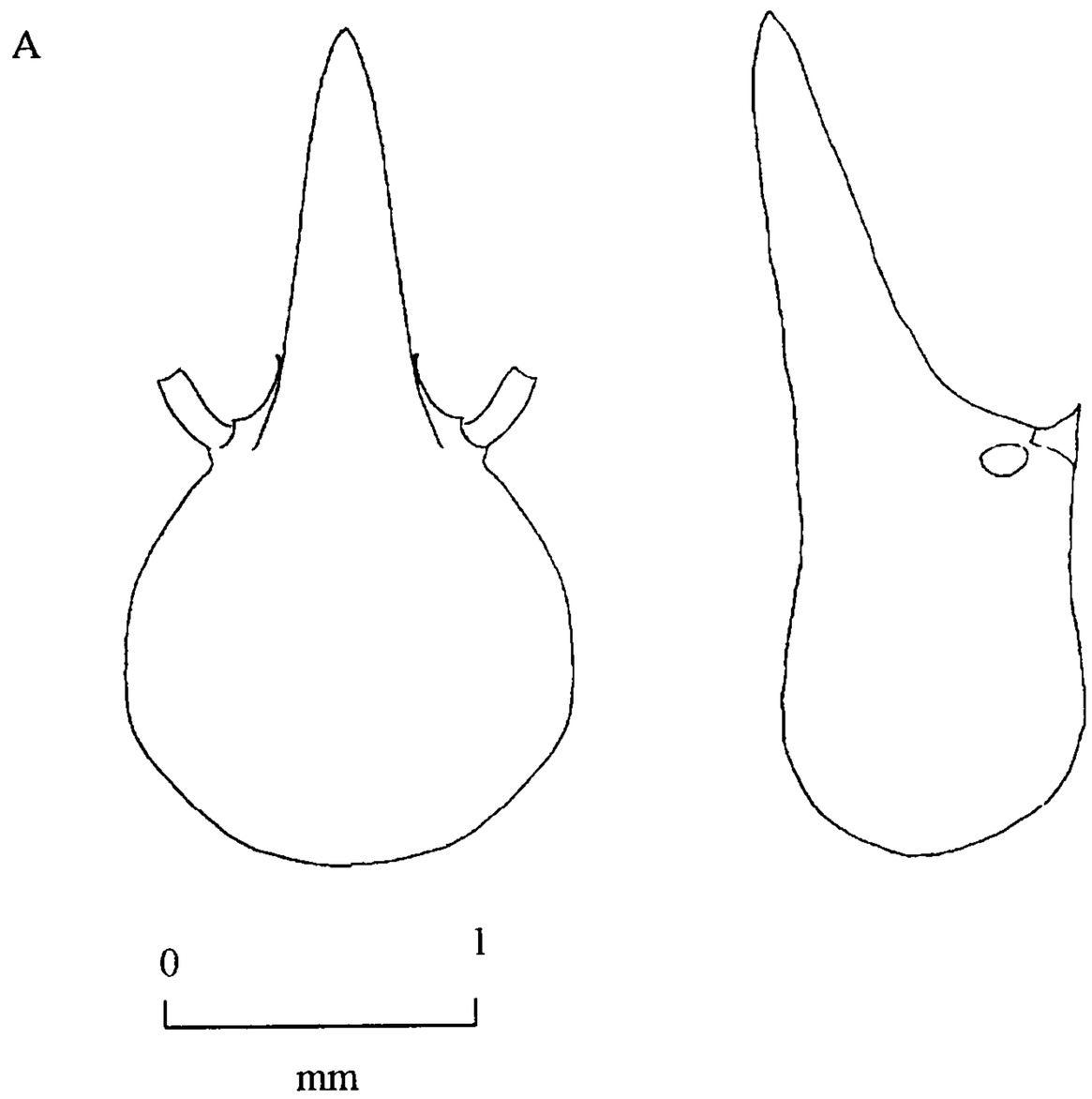


Figure 4.5
Hirtitermes brabazoni A: Soldier head capsule
B: Worker mandibles

Leucopitermes Emerson

Leucopitermes thoii new species

Etymology

This species is named after Dr. Tho Yow Pong, the greatest Southeast Asian taxonomist of the 20th century, who first recorded this species.

HOLOTYPE. One specimen soldier caste. From dead wood, Ketambe field station, Aceh Tenggara, Indonesia. coll. Sugesti, September 1998. Deposited in Bogor Zoological Museum, Bogor, Indonesia.

PARATYPES. Soldiers, workers. From dead wood, Ketambe field station, Aceh Tenggara, Indonesia. coll. Sugesti, September 1998. Deposited in Bogor Zoological Museum, Bogor, Indonesia.

Soldiers, workers. From dead wood, Ketambe field station, Aceh Tenggara, Indonesia. coll. Hasballah, Sugesti, Syaukani, Gathorne-Hardy, September 1998. Deposited in Syiah Kuala University, Darussalam, Banda Aceh, Indonesia.

Soldiers, workers. From dead wood, Ketambe field station, Aceh Tenggara, Indonesia. coll. Hasballah, Sugesti, Syaukani, Gathorne-Hardy, September 1998. Deposited in the Natural History Museum, London, U.K.

Habitat-Undisturbed lowland tropical rainforest. Found in very rotten dead wood.

Soldier

Head capsule yellowish brown to orange, nasus darker brown, antennae pale brown, pronotum pale brown, legs yellowish brown. Head capsule shape in plan view is almost square-shaped, bulging slightly behind the bases of the antennae. Nasus conical, shorter than head capsule without nasus. Antennae with 13 segments. Postmentum is convex and the sides are more or less uniformly concave, with very few setae. Pronotum in plan view indented in middle, outer corners rounded and not extended. In profile, anterior lobe is smaller than the posterior.

Table 4.6

Soldiers, 17 specimens from 2 nests	Range (mm)	Mean (mm)	S.D.
Head Length	1.75-2.12	1.97	0.11
Head width	1.05-1.33	1.21	0.1
Head length to base of rostrum	1.16-1.42	1.27	0.08
Rostrum length	0.59-0.78	0.7	0.06
Rostrum: head ratio	0.44-0.62	0.56	0.05
Head width: length ratio	0.91-0.99	0.96	0.03

Worker

Head capsule pale yellow, darkest part of antennal flagellum and pronotum are pale yellow, legs are pale yellow, abdominal tergites are transparent. Head is oval with sparse setae. Thirteen antennal articles. Pronotum saddle-shaped. Abdomen covered by setae.

Left mandible apical tooth is roughly equal in prominence to the first marginal, second marginal tooth is absent, incorporated into the cutting edge

between the first and third. Third marginal tooth distinctly protrudes from the cutting edge of the first plus second, the anterior edge is shorter than that of the first and is separated from the molar prominence by a distinct gap. The fourth marginal tooth is indistinct

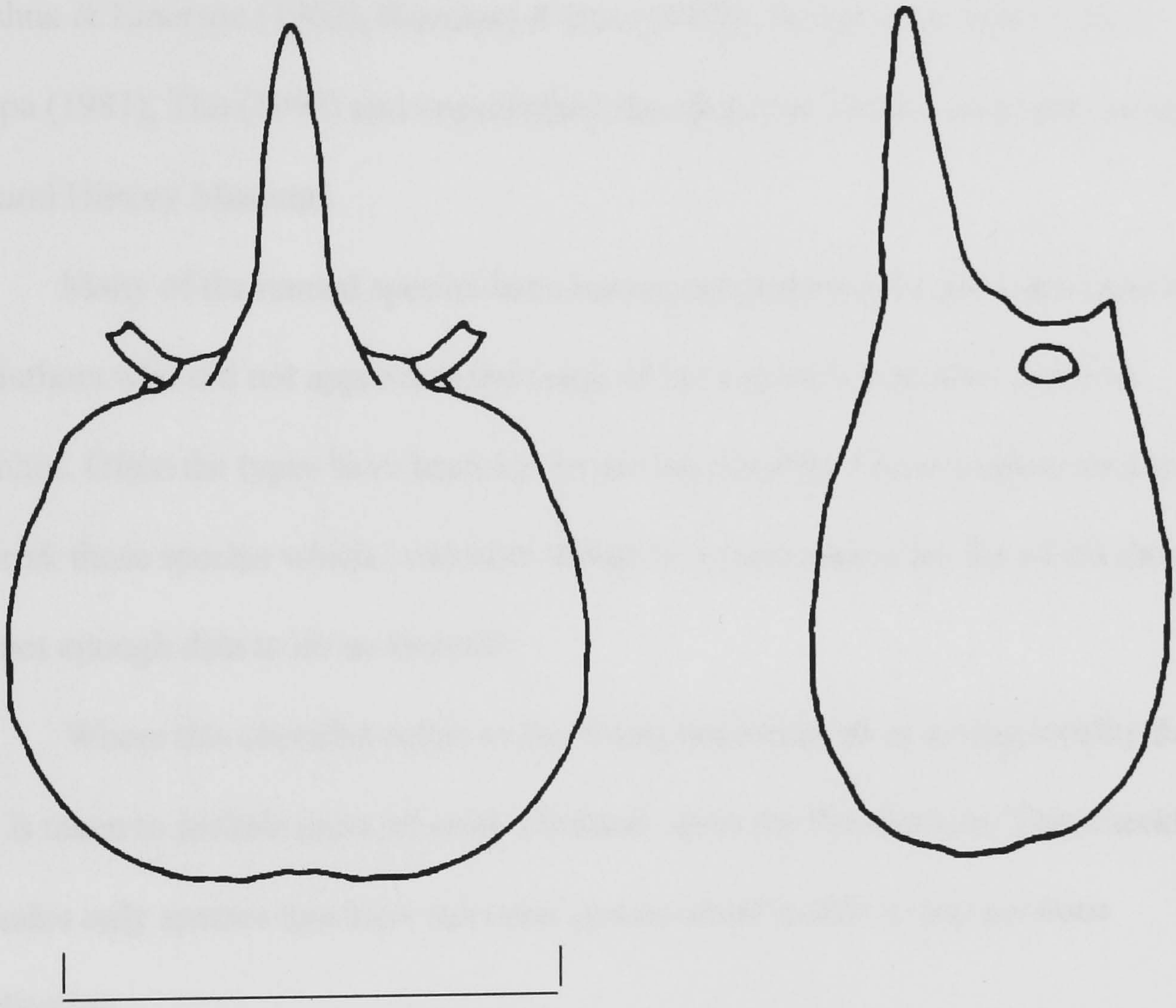
Right apical tooth is same length as the first marginal (all measurements follow those of Roonwal, 1970). The first marginal anterior edge is uniform and longer than that of the second. The second marginal tooth is fully developed and separate from the first, the posterior edge of the first marginal tooth is longer than that of the second. Cockroach notch at proximal end of right molar plate is weakly developed and shallowly obtuse. The molar plate ridges are evident and number eight.

The gut structure of *Leucopitermes* is illustrated by Roisin & Pasteels (1996) page 578.

Table 4.7

Workers. 11 specimens from 2 nests	Range (mm)	Mean (mm)	S.D.
Right mandible, Apical tooth to 1st marginal	0.055-0.089	0.07	0.009
Right mandible, Apical tooth to 2nd marginal	0.135-0.195	0.16	0.016
Right mandible 1st to 2nd marginal	0.072-0.111	0.09	0.011
Right mandible index	0.66-0.9	0.77	0.084
Left mandible, apical tooth to 1st marginal	0.05-0.072	0.06	0.007
Left mandible, apical tooth to 3rd marginal	0.17-0.241	0.21	0.019
Left mandible, 1st to 3rd marginal	0.127-0.176	0.15	0.014
Left mandible index	0.356-0.48	0.428	0.042

Comparisons: *L. thoii* can easily be separated from the other *Leucopitermes* species, *L. leucops*. *L. thoii* has a large, rectangular (almost square) head capsule, while that of *leucops* is almost round. *Leucopitermes* is often confused with *Nasutitermes*. These genera can be separated by the fact that the soldiers of *Leucopitermes* have an unsclerotised abdomen, while those of *Nasutitermes* are sclerotised. The right worker mandible of *Leucopitermes* shows a cockroach notch, which is absent in *Nasutitermes*.



B

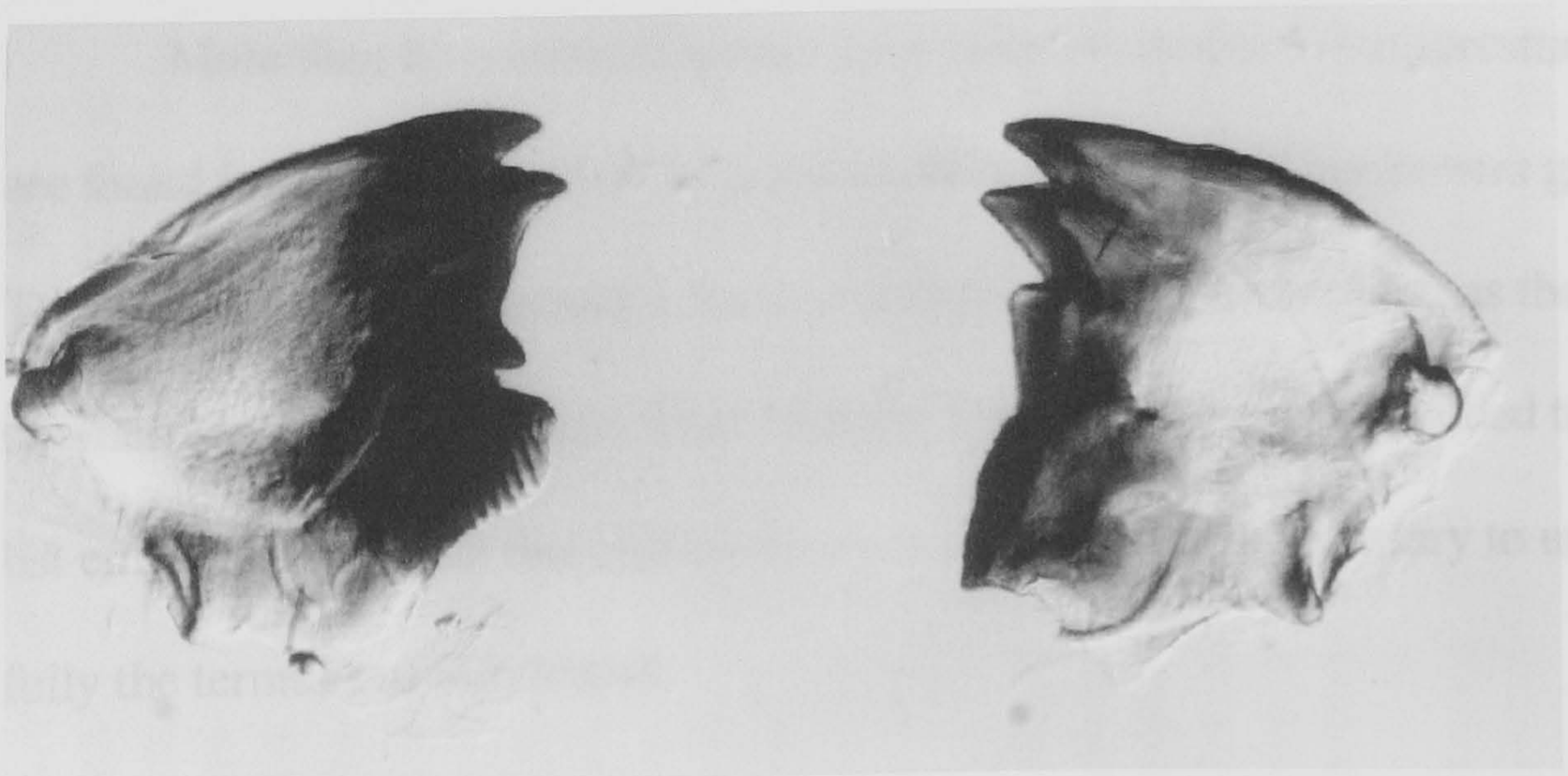


Figure 4.6
Leucopitermes thoii
A: Soldier head capsule
B: Worker mandibles

The Appendix contains a checklist of all species found in Sundaland and their locality data, from the following sources: Ahmad (1968), Bose (1980), Collins (1979, 1980, 1984), Eggleton *et al.* (1999), Emerson (1960), Gathorne-Hardy *et al.* (2000, 2001), Harris (1957, 1968), Haviland (1898), Hoare & Jones (1998), Homathevi (2000), Holmgren (1911-14), John (1925), Jones (1996, 2000), Jones & Brendell (1998), Jones & Prasetyo (in press), Jones *et al.* (in prep), Kalshoven (1960), Kemner (1934), Krishna (1956,1965, 1972, 2001), Krishna & Adams (1982), Krishna & Emerson (1962), Roonwal & Bose (1970), Roonwal & Maiti (1966), Thapa (1981), Tho (1992) and unpublished data from the Termite Research Group, Natural History Museum.

Many of the named species have inadequate descriptions and were described by authors who did not appreciate the range of intra-specific variation found in termites. Often the types have been lost or are inaccessible. I have marked with an asterisk those species which I consider should be synonomised but for which there are not enough data to do so formally.

Where this checklist refers to the Malay peninsula when giving locality data, this is taken to include parts of south Thailand, up to the Kra ecotone. This checklist includes only species that have not been synonomised in this or any previous publication.

More than 80 unnamed species have been referred to in the literature. These are found in almost all genera but particularly in the *Termes/Capritermes* group of Termitinae. I have not included these morphospecies in the checklist, as their taxonomic status is uncertain. That a further 25% of species can be added to the total list emphasises the fact that serious revisionary taxonomy is necessary to understand fully the termites of Sundaland.

Appendix 4.1: A Checklist of the termites found in the Sunda region.

Genus	Species	Author	Year	Distribution
Kalotermitidae				
Neotermes	*artocarpi*	(Haviland)	1897	Sarawak
Neotermes	*dalbergiae*	(Kalshoven)	1930	Java
Neotermes	*minutus*	Thapa	1981	Sabah
Neotermes	*sonneratiae*	Kemner	1934	W. Java
Neotermes	*tectonae*	(Dammerman)	1915	Java, Sumatra, Sabah, Malay Peninsula
Cryptotermes	*cynocephalus*	Light	1921	West Java, SE Kalimantan, Sarawak, Sabah, Malay Peninsula
Cryptotermes	*domesticus*	(Haviland)	1898	Malay peninsula, Sumatra, Sarawak
Cryptotermes	*dudleyi*	Banks	1918	Java, Sumatra, Malay peninsula
Cryptotermes	*sumatrensis*	Kemner	1930	Sumatra
Cryptotermes	*sukauensis*	Thapa	1981	Sabah
Cryptotermes	*thailandis*	Ahmad	1963	Malay peninsula
Postelectrotermes	*tongyaii*	Ahmad	1965	Malay peninsula
Glyptotermes	*besarensis*	Thakur & Thakur	1992	Krakatau
Glyptotermes	*borneensis*	(Haviland)	1898	Sarawak, Malay Peninsula
Glyptotermes	*brevicaudatus*	(Haviland)	1898	Malay Peninsula, Borneo, Sumatra
Glyptotermes	*buttel reepeni*	(Holmgren)	1913	Malay Peninsula
Glyptotermes	*caudominutus*	Kemner	1934	Java
Glyptotermes	*chatterjii*	Thapa	1981	Sabah
Glyptotermes	*concavifrons*	Krishna & Emerson	1962	Java
Glyptotermes	*dentatus*	(Haviland)	1898	Sarawak, Sabah, Malay peninsula
Glyptotermes	*kachongensis*	Ahmad	1965	Malay peninsula
Glyptotermes	*kirkbyi*	Krishna & Emerson	1962	Sumatra
Glyptotermes	*kunakensis*	Thapa	1981	Sabah

Glyptotermes	*laticaudomunitus*	Thapa	1985 Sabah
Glyptotermes	*minutus*	Kemner	1930 Krakatau
Glyptotermes	*montanus*	Kemner	1934 W. Java
Glyptotermes	*neoborneensis*	Thapa	1981 Sabah
Glyptotermes	*niger*	Kemner	1934 W. Java
Glyptotermes	*panaitanensis*	Thakur & Thakur	1992 Panaitan Is
Glyptotermes	*paracaudomunitus*	Thapa	1981 Sabah
Glyptotermes	*paratuberculatus*	Thapa	1981 Sabah, N. Sumatra
Glyptotermes	*pinagae*	(Haviland)	1898 Sarawak, Sabah, Malay peninsula
Glyptotermes	*sepilokensis*	Thapa	1981 Sabah
Glyptotermes	*tuberculatus*	Froggart	1896 N. Sumatra
Rhinotermitidae			
Heterotermes	*tenuior*	(Haviland)	1898 Borneo, Sumatra, Malay Peninsula
Coptotermes	*elisae*	Desneux	1905 Java, Sumatra, Malay peninsula, Sabah, Sarawak
Coptotermes	*gestroi*	(Wasman)	1896 Java, Malay Peninsula, Sarawak
Coptotermes	*kalshoveni*	Kemner	1934 Java, Sumatra, Malay Peninsula, Central and South Kalimantan
Coptotermes	*sepangensis*	Krishna	1956 Sabah, Central and South Kalimantan, Sumatra
Coptotermes	*sinabangensis*	Oshima	1923 Sumatra, Malay Peninsula
Coptotermes	*travians*	(Haviland)	1898 Sumatra, Malay Peninsula, Borneo, Java
Termitogeton	*planus*	(Haviland)	1898 Sarawak, Sabah, Malay peninsula, Sumatra
Stylotermes	*roonwali*	Thapa	1981 Sabah, Brunei
Prorhinotermes	*flavus*	Buignon & Popoff	1910 Throughout the region, coastal areas
Parrhinotermes	*aequalis*	(Haviland)	1898 Borneo, Malay peninsula, Sumatra
Parrhinotermes	*buttel reepeni*	Holmgren	1913 Sabah, Sarawak, Central Kalimantan, Sumatra, Malay peninsula,
Parrhinotermes	*inaequalis*	(Haviland)	1898 Sarawak, Malay Peninsula, Sabah, Sumatra

Parrhinotermes	*microdentiformis*	Thapa	1981 Sabah, Central and West Kalimantan, Malay Peninsula, North Sumatra, Central Sumatra
Parrhinotermes	*microdentiformisoides*	Thapa	1981 Sabah, Central Kalimantan, Malay Peninsula, North Sumatra
Parrhinotermes	*minor*	Thapa	1981 Sabah, Central and South Kalimantan, Malay Peninsula, Central Sumatra
Parrhinotermes	*pygmaeus*	John	1925 Malay Peninsula, Sabah, North and East Sumatra, Siberut
Schedorhinotermes	*brevialatus*	(Haviland)	1898 Throughout the region
Schedorhinotermes	*holmgreni*	Emerson	1949 Sumatra
Schedorhinotermes	*maximus*	(Holmgren)	1913 S. E. Borneo
Schedorhinotermes	*medioobscurus*	(Holmgren)	1914 Throughout the region
Schedorhinotermes	*malaccensis*	(Holmgren)	1913 Throughout the region
Termitidae			
Apicotermitinae			
Euhamitermes	*hamatus*	(Holmgren)	1912 Malay peninsula
Orientotermes	*emersoni*	Ahmad	1976 Sarawak, Brunei
Termitinae			
Protohamitermes	*globiceps*	Holmgren	1913 Sarawak, Brunei, Sabah, South and Central Kalimantan, Malay Peninsula
Prohamitermes	*hosei*	(Desneux)	1905 Sarawak, Sabah, South Kalimantan
Prohamitermes	*mirabilis*	(Haviland)	1898 Throughout the region
Labritermes	*buttel reepeni*	Holmgren	1913 Sumatra, Malay peninsula, Sarawak, Sabah, Central and South Kalimantan
Labritermes	*emersoni*	Krishna & Adams	1982 Sarawak, Sabah, Central Kalimantan, Malay Peninsula, N. Sumatra
Labritermes	*kistneri*	Krishna & Adams	1982 Sarawak, Sabah, West and Central Kalimantan, Malay peninsula, N. Sumatra
Amitermes	*dentatus*	(Haviland)	1898 Malay peninsula, Sumatra, Sabah, Sarawak
Globitermes	*globosus*	(Haviland)	1898 Borneo, Malay peninsula, Sumatra

Globitermes	*sulphurens*	(Haviland)	1898	Malay peninsula
Globitermes	*vadaensis*	Kemner	1934	East Java
Microcerotermes	*crassus*	Snyder	1934	Malay peninsula
Microcerotermes	*dammermani*	Roonwal & Maiti	1966	Durian, in Rhio archipelago
Microcerotermes	*depokensis*	Kemner	1934	Depok
Microcerotermes	*distans*	(Haviland)	1898	Borneo, Malay peninsula
Microcerotermes	*dubius*	(Haviland)	1898	Borneo, Malay peninsula, S Sumatra
Microcerotermes	*havilandi*	Holmgren	1913	Borneo, Sumatra, Malay Peninsula
Microcerotermes	*madurae*	Kemner	1934	Madura
Microcerotermes	*paracelebensis*	Ahmad	1965	Malay Peninsula
Microcerotermes	*serrula*	(Desneux)	1904	Borneo, Malay Peninsula, N & C. Sumatra, Siberut
Termes	*brevicornis*	Haviland	1898	Sarawak
Termes	*comis*	Haviland	1898	Sarawak, South Kalimantan, Malay peninsula, S & C Sumatra, Siberut
Termes	*laticornis*	Haviland	1898	Sarawak, South Kalimantan, Sumatra, Malay Peninsula
Termes	*major*	Morimoto	1973	Malay peninsula
Termes	*propinquus*	(Holmgren)	1914	Malay peninsula, Sumatra, South Kalimantan, Sabah, Brunei and Sarawak
Termes	*rostratus*	Haviland	1898	Sarawak, Central Kalimantan, S Sumatra, Malay peninsula
Coxocapritermes	*orientalis*	Ahmad & Akhtar	1981	Malay peninsula, Sumatra, Sabah, Sarawak, Central & South Kalimantan, Siberut
Kemneritermes	*sarawakensis*	Ahmad & Akhtar	1981	Sarawak, Sabah, Central & South Kalimantan, N & C Sumatra
Mirocapritermes	*connectens*	Holmgren	1914	Sumatra, Malay peninsula, Sarawak, Sabah, Central and South Kalimantan
Mirocapritermes	*latignathus*	Ahmad	1965	Malay Peninsula
Oriencapritermes	*kluangensis*	Ahmad & Akhtar	1981	Malay peninsula, Central and South Kalimantan

Procapritermes	*atypus*	Holmgren	1913	Sarawak, Sabah, South Kalimantan, W. Sumatra
Procapritermes	*minutus*	(Haviland)	1898	Sarawak, Sabah, Central and South Kalimantan, C. Sumatra
Procapritermes	*neosetiger*	Thapa	1981	Sabah, Central & South Kalimantan, C. Sumatra
Procapritermes	*sandakanensis*	Thapa	1981	Sabah, C. Sumatra
Procapritermes	*setiger*	(Haviland)	1898	Sarawak, Sabah, Malay Peninsula, C. Sumatra
Procapritermes	*longignathus*	(Ahmad)	1965	Malay peninsula
Procapritermes	*prosetiger*	(Ahmad)	1965	Borneo, Malay Peninsula, C. Sumatra, Siberut
Homallotermes	*eleanorae*	Krishna	1972	Malay peninsula, Sabah, Sarawak, Brunei, Central Kalimantan, N & C Sumatra
Homallotermes	*exiguus*	Krishna	1968	Borneo, N. Sumatra
Homallotermes	*foraminifer*	(Haviland)	1898	Malay peninsula, Sabah, Sarawak, Central Kalimantan, C. Sumatra
Pericapritermes	*brachygnathus*	(John)	1925	Malay peninsula
Pericapritermes	*buitenzorgi*	(Holmgren)	1914	W. Java, Malay peninsula
Pericapritermes	*dolichocephalus*	(John)	1925	Malay peninsula, Sabah, Sarawak, Central Kalimantan, C.& S. Sumatra, Siberut
Pericapritermes	*latignathus*	(Holmgren)	1914	W. Java, Malay peninsula, Sabah, South Kalimantan, N. Sumatra, Siberut
Pericapritermes	*modiglianii*	(Silvestri)	1922	Sumatra
Pericapritermes	*mohri*	(Kemner)	1934	W. Java, Malay peninsula, Sabah, South Kalimantan, Sarawak, N. Sumatra
Pericapritermes	*nitobei*	(Shiraki)	1909	Malay peninsula, Borneo, Sumatra, Siberut
Pericapritermes	*semarangi*	(Holmgren)	1913	West and Central Java, Sumatra, Sabah, Malay Peninsula, Brunei, South Kalimantan
Pericapritermes	*speciosus*	(Haviland)	1898	Malay peninsula, Sarawak, Sabah, N. Sumatra, South Kalimantan
Dicuspiditermes	*cacuminatus*	Krishna	2001	Malay peninsula
Dicuspiditermes	*fissifex*	Krishna	2001	Malay peninsula, C & N Sumatra
Dicuspiditermes	*kistneri*	Krishna	2001	Malay peninsula

Dicuspiditermes	*laetus*	Silvestri	1914 Malay peninsula
Dicuspiditermes	*minutus*	Akhtar & Riaz	1992 Malay peninsula, Brunei, East Kalimantan
Dicuspiditermes	*nemorosus*	(Haviland)	1898 Malay peninsula, Borneo, Sumatra, Siberut
Dicuspiditermes	*paramakhamensis*	Thapa	1981 Sabah
Dicuspiditermes	*rothi*	(Holmgren)	1913 Sarawak
Dicuspiditermes	*santschii*	(Silvestri)	1922 Sumatra, Malay peninsula, Sabah
Pseudocapritermes	*parasilvaticus*	(Ahmad)	1965 N. Sumatra
Pseudocapritermes	*silvaticus*	Kemner	1934 Java, Sarawak
Syncapritermes	*greeni*	(John)	1925 Malay peninsula
Macrotermitinae			
Macrotermes	*ahmadi*	Tho	1975 Malay peninsula, N. & C. Sumatra
Macrotermes	*carbonarius*	(Hagen)	1858 Borneo, Malay peninsula
Macrotermes	*gilvus*	(Hagen)	1858 Throughout the region
Macrotermes	*malaccensis*	(Haviland)	1898 Malay peninsula, Sumatra, Borneo
Odontotermes	*billitoni*	Holmgren	1913 Java, Sumatra, Siberut, Central Kalimantan
Odontotermes	*bogoriensis*	(Kemner)	1934 Java
Odontotermes	*butteli*	Holmgren	1913 Malay peninsula
Odontotermes	*denticulatus*	Holmgren	1913 Malay peninsula, Sabah, Sarawak, South Kalimantan, C. Sumatra
Odontotermes	*dives*	(Hagen)	1858 Throughout the region
Odontotermes	*feae*	(Wasmann)	1896 Malay peninsula
Odontotermes	*grandiceps*	Holmgren	1913 W. & E. Java, Malay Peninsula, Sumatra, Sabah
Odontotermes	*hageni*	(Holmgren)	1913 Borneo
Odontotermes	*incisus*	Holmgren	1913 Sumatra
Odontotermes	*indrapurensis*	Holmgren	1913 Sumatra
Odontotermes	*javanicus*	Holmgren	1913 Sumatra, Malay peninsula, W. Java, Sarawak, Sabah, Siberut
Odontotermes	*karawajevi*	John	1925 W. Java
Odontotermes	*karnyi*	Kemner	1934 W. Java
Odontotermes	*makassarensis*	Kemner	1934 Bali (Lake Bratan)

Odontotermes	*malaccensis*	Holmgren	1913 Malay peninsula.
Odontotermes	*minutus*	Amir	1975 W. Java, Sumatra, Sabah, Central Kalimantan
Odontotermes	*neodenticulatus*	Thapa	1981 Sabah, South Kalimantan
Odontotermes	*oblongatus*	Holmgren	1913 Malay peninsula, Sabah, West Kalimantan, N. Sumatra
Odontotermes	*prodives*	Thapa	1981 Sabah
Odontotermes	*proformosanus*	Ahmad	1965 Malay peninsula
Odontotermes	*sarawakensis*	Holmgren	1913 Sarawak, South Kalimantan, Malay peninsula, Sabah, N & C Sumatra
Odontotermes	*taprobanes*	(Hagen)	1858 Borneo, Malay peninsula
Odontotermes	*takensis*	Ahmad	1965 Malay peninsula
Hypotermes	*sumatrensis*	Holmgren	1913 Sumatra
Hypotermes	*xenotermitis*	(Wasmann)	1896 Malay peninsula, Sabah, South Kalimantan, Siberut
Microtermes	*obesi*	Holmgren	1913 Malay Peninsula
Ancistrotermes	*pakistanicus*	(Ahmad)	1965 Malay peninsula, Java, C. Sumatra, South Kalimantan
Nasutitermitinae			
Ceylonitermes	*indicola*	Thakur	1976 N. Sumatra, Siberut
Hirtitermes	*hirtiventris*	Holmgren	1913 Sarawak, Sabah, Central Kalimantan, N. Sumatra
Hirtitermes	*spinocephalus*	(Oshima)	1914 Sabah
Hirtitermes	*brabazoni*	Gathorne-Hardy	2001 Central Kalimantan
Nasutitermes	*atripennis*	(Haviland)	1898 Malay peninsula, Sarawak, Sabah, South Kalimantan, N. Sumatra
Nasutitermes	*proatripennis*	(Ahmad)	1965 Malay peninsula, C. Sumatra
Nasutitermes	*acutus*	(Holmgren)	1913 Java, Sumatra, Malay peninsula
Nasutitermes	*corporaali*	(Wasmann)	1922 Java
Nasutitermes	*dimorphus*	Ahmad	1965 Malay peninsula
Nasutitermes	*fuscipennis*	(Haviland)	1898 Malay peninsula, Sarawak, Sabah
Nasutitermes	*havilandi*	(Desneux)	1904 Malay peninsula, Sarawak, Sabah, Sumatra
Nasutitermes	*jacobsoni*	Oshima	1923 Sumatra

Nasutitermes	*johoricus*	(John)	1925	Malay peninsula, S. Sumatra, Central Kalimantan
Nasutitermes	*longinasus*	(Holmgren)	1913	Malay peninsula, Sabah, Sarawak, Central & South Kalimantan, N. Sumatra, Siberut
Nasutitermes	*longinasoides*	Thapa	1981	Sabah, N. Sumatra
Nasutitermes	*longinostris*	(Holmgren)	1913	Sarawak, Sabah, South Kalimantan
Nasutitermes	*matangesis*	(Haviland)	1898	Everywhere in the region
Nasutitermes	*neoparvus*	Thapa	1981	Sabah, Malay peninsula, Brunei, Central and South Kalimantan, N. Sumatra
Nasutitermes	*ovipennis*	(Haviland)	1898	Sabah, Sarawak, Malay peninsula
Nasutitermes	*perparvus*	Ahmad	1965	Malay peninsula
Nasutitermes	*rectangularis*	Thapa	1981	Sabah
Nasutitermes	*sandakanensis*	(Oshima)	1914	East Kalimantan
Nasutitermes	*simularis*	Oshima	1923	Sumatra
Nasutitermes	*tungsalangensis*	Ahmad	1965	Malay peninsula
Bulbitermes	*borneensis*	(Haviland)	1898	Sarawak, Sabah, N.& S. Sumatra, Siberut
Bulbitermes	*constrictiformis*	(Holmgren)	1914	Malay peninsula, Sabah, Sumatra
Bulbitermes	*constrictoides*	(Holmgren)	1913	W. Java, Sabah, Malay peninsula
Bulbitermes	*constrictus*	(Haviland)	1898	Sarawak, Sabah, Central Kalimantan, N. Sumatra
Bulbitermes	*durianensis*	Roonwal & Maiti	1966	Durian Is.
Bulbitermes	*flavicans*	(Holmgren)	1913	Sarawak, Sabah, Central Kalimantan, Sumatra, Malay peninsula, Siberut
Bulbitermes	*gedeensis*	(Kemner)	1934	W. Java
Bulbitermes	*lakshmani*	Roonwal & Maiti	1966	W. Java
Bulbitermes	*nasutus*	(Holmgren)	1913	Sumatra
Bulbitermes	*perpusillus*	(John)	1925	Malay peninsula, W. Java
Bulbitermes	*prabhae*	Krishna	1965	Malay peninsula, C. Sumatra
Bulbitermes	*rosae*	(Kemner)	1934	W Java
Bulbitermes	*salakensis*	Krishna	1934	W Java

Bulbitermes	*sarawakensis*	(Haviland)	1898	Sarawak, Sabah, Malay peninsula, Sumatra
Bulbitermes	*singaporiensis*	(Haviland)	1898	Malay peninsula, Borneo, N. Sumatra
Bulbitermes	*subulatus*	(Holmgren)	1913	Sumatra
Bulbitermes	*vicinus*	(Kemner)	1934	W. Java
Lacessititermes	*albipes*	(Haviland)	1898	Borneo, Java
Lacessititermes	*batavus*	Kemnner	1934	W. Java
Lacessititermes	*breviarticulatus*	(Holmgren)	1913	Borneo
Lacessititermes	*laborator*	(Haviland)	1898	Sarawak, Malay peninsula, Sumatra
Lacessititermes	*lacessitiformis*	(Holmgren)	1898	Sarawak
Lacessititermes	*lacessitus*	(Haviland)	1898	Malay peninsula
Lacessititermes	*pilferus*	(Holmgren)	1913	Borneo
Lacessititermes	*sordidus*	(Haviland)	1898	Sarawak
Lacessititermes	*luzonensis*	(Oshima)	1917	W. Java
Longipedidtermes	*longipes*	(Haviland)	1898	Sumatra, Borneo, Malay peninsula
Longipedidtermes	*kistneri*	Akhtar & Ahmad	1985	W. Java, N. Sumatra
Hospitalitermes	*asahinai*	Morimoto	1973	Malay peninsula
Hospitalitermes	*ataramens*	Prashad & Sen-Sarma	1960	Malay peninsula
Hospitalitermes	*bicolor*	(Haviland)	1898	C. Java, Malay peninsula
Hospitalitermes	*birmanicus*	(Snyder)	1934	Malay peninsula
Hospitalitermes	*ferrugineus*	(John)	1925	Sumatra
Hospitalitermes	*flaviventris*	(Wasmann)	1902	Malay peninsula, Borneo
Hospitalitermes	*grassii*	Ghidini	1937	Sumatra
Hospitalitermes	*hospitalis*	(Haviland)	1898	Malay peninsula, Borneo, Sumatra, Siberut
Hospitalitermes	*lividiceps*	(Holmgren)	1913	East and South Kalimantan
Hospitalitermes	*rufus*	(Haviland)	1913	Malay peninsula, Sabah, Sarawak, W. Java, N. Sumatra
Hospitalitermes	*umbrinus*	(Haviland)	1898	Throughout the region
Aciculitermes	*aciculatus*	(Haviland)	1898	Sarawak
Subulioiditermes	*emersoni*	Ahmad	1968	Sarawak

Subulioiditermes	*subulioides*	Ahmad	1968	Sarawak, Sabah, Malay peninsula, S. Sumatra
Eleanoritermes	*borneensis*	Ahmad	1968	Sarawak
Malaysiotermes	*spinocephalus*	Ahmad	1968	Throughout the region
Malaysiotermes	*holmgreni*	(Ahmad)	1968	Borneo, Malay peninsula, Sumatra
Leucopitermes	*leucops*	(Holmgren)	1914	Throughout the region
Leucopitermes	*thoii*	Gathorne-Hardy	This MS	Malay peninsula, N.& S. Sumatra
Oriensubulitermes	*inanis*	(Haviland)	1898	Malay peninsula, Borneo, Sumatra
Oriensubulitermes	*kemneri*	Ahmad	1968	Sarawak
Sabahitermes	*leuserensis*	(Gathorne-Hardy)	2001	N. Sumatra, Malay peninsula
Sabahitermes	*malakuni*	Thapa	1996	Sarawak, Sabah

Chapter 5. Quaternary Rainforest Refugia in Southeast Asia; using termites (Isoptera) as indicators

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5.1 Introduction

The rainforests of Southeast Asia are among the most biodiverse areas in the world (Myers *et al.,* 2000). They are a dynamic ecosystem, and palynological evidence indicates that they were considerably affected by Quaternary glaciations (Kaars & Dam 1995, Morley 2000). During glaciations most of the vegetation was probably a mixture of savannah and patchy deciduous forest (Morley 2000). Obligate rainforest species are likely to have been confined to a few refugia in northern Borneo, northern Sumatra and the Mentawai islands (Brandon-Jones 1998). During interglacials rainforest recolonised the region (Kaars & Dam 1995, Morley 2000).

The extent of vegetation change and the sites of lowland rainforest refugia have never been fully investigated. Here I use termite data to determine the locations and to try and assess the geographical limits of the refugia. I used palynological, geological, fossil and present plant and mammal distribution data to define potential refugium sites and then examined termite survey data from these areas to assess the suitability of termites as indicators of Quaternary climate change.

Termite data from a complete survey of the region were then examined to provide an indication of the possible extent of the rainforest refugia.

Termites are easily sampled (Jones & Eggleton 2000). They are sensitive to disturbance, especially to forest canopy loss (Dibog *et al.* 1999, Eggleton *et al.* 1996; 1997, Chapter 3), and in general they are poor at crossing biogeographical barriers (Abe, 1984, Gathorne-Hardy *et al.* 2000, chapters 1 & 2). Termite composition is known to reflect historical patterns (Eggleton *et al.* 1994, Eggleton 2000, Davies 2001), making them ideal organisms with which to investigate the ongoing effects of Quaternary climate change.

The Quaternary

The Quaternary is characterised by having been a great many (more than a hundred) glaciation events (Nesje & Dahl 2000). The change from the predominantly warm climate of rest of the Tertiary was probably caused by the uplift of the Himalayan/Tibetan and the Colorado plateaux, as well as the closure of the Panama isthmus and the deepening of the Bering straits, which displaced atmospheric and ocean circulation (Ruddiman & Kutzbach 1990, Ruddiman & Raymo 1988). These tectonic changes are thought to have brought the global climate to a threshold at which variations in insolation (the Milankovitch effect) can have an effect (Maslin *et al.* 1998, Nesje & Dahl 2000). There is still debate about the exact processes which started and controlled the timings of Quaternary glaciations (Maslin *et al.* 1998, Prueher & Rea 1998, Rutherford & D'Hondt 2000).

Traditionally the climate of the Quaternary has been divided up into two categories: glacials and interglacials. However, this has been found to be too simplistic, so deep ocean oxygen isotope stages, which correlate with the amount of terrestrial ice are nowadays used to provide a coherent system of referring to the fluctuations in global temperature. The Quaternary had five severe glacial episodes (O isotope stages 2, 6, 12, 16 and 22), the most recent being the last glacial maximum (LGM, within O isotope stage 2) which occurred between about 22,000 and 11,500 years before present (BP).

Most of what I discuss will be concerned with the last glacial cycle (isotope stages 5-1), about which there are most data.

Quaternary climate change in the Sunda region.

Monsoons

The climate of Southeast Asia is primarily governed by monsoon winds (Whitmore 1984). The winter or north-west monsoon is caused by air from cold high pressure areas in Siberia and the Tibetan plateau blowing to the hot low pressure zone over Australia. The monsoon picks up water from the West Pacific Warm Pool and the South China Sea (SCS) and is the cause of most of the rainfall in the Sunda region (Whitten *et al.* 1984; 1996, MacKinnon *et al.* 1997, An 2000). The summer or south-east monsoon works in the opposite way to the winter one, it picks up water from the Indian ocean, causing rain in the summer months (An 2000). However, the mountains of Nusa Tenggara, Java and the Barisan Range of Sumatra cause a rain-shadow

effect, making the summer a relatively dry season for most of the region (Whitten *et al.* 1984, MacKinnon *et al.* 1997).

Analysis of loess deposits shows that during higher latitude glacials the northern summer was colder than during interglacials, so the atmospheric pressure was higher over continental Asia, which led to a reduced summer monsoon (An 2000). The winter monsoon was probably stronger than it is now (An 2000). This reduction of the summer monsoon may have caused an increase in seasonality during Oxygen Isotope Stages 4, 3 and 2.

Temperature

Pollen core and oxygen isotope data from the *Globigerinoides* foraminifera can provide evidence of past temperatures. The temperature in Southeast Asia of oxygen isotope stage 5 was probably similar to that of today, or at times a little higher (Kaars & Dam 1995, Pelejero *et al.* 1999) or a little lower (Pelejero *et al.* 1999, Lee *et al.* 1999). In isotope stages 4 and 3 it declined by between 2°C (Pelejero *et al.* 1999) and 4°C (Kaars & Dam 1995), the former being the more likely. The temperature in isotope stage 2 (the last glacial maximum, or LGM) was between 3°C and 7°C lower than present. The consensus (using all available data) is that the decrease at sea level was about 4°C (Morley 2000).

Sea level

Bard *et al.* (1991), Shackleton (1987), Haq *et al.* (1987) and Pirazzoli *et al.* (1991) have estimated sea levels for pre-Holocene times. These estimates are inevitably open to error at smaller scale (Shackleton 1987) but though they use different methods, in general they agree with each other. During interglacials the sea level was approximately the same as it is now, during stages 3 and 4 it dropped by about 40-50 m (or more). It was about 120 m lower than present sea level at the LGM (Shackleton 1987, Pirazzoli *et al.* 1991, Voris 2000), exposing about 1800000 km^2 of the Sunda shelf.

The expansion of the exposed Sunda shelf in the LGM, preventing the winter monsoon from picking up moisture from the SCS probably led to increased drought in the central part of the Sunda region. This drought and increased seasonality is thought to have changed the vegetation of the central part of the Sunda shelf, causing it to become savannah-like (Medway 1972, Morley 2000).

Evidence for climate change

Palynological, geological, fossil and modern animal distributions all provide evidence of Pleistocene climate change. Table 5.1 shows sites for which there is direct evidence of climate change affecting the biota of Southeast Asia. In most of these areas it is thought that the flora changed to a savannah or wooded savannah system.

Areas of continuing rainforest

Though the whole of Southeast Asia is likely to have felt the effects of the increased seasonality of stages 4, 3 and 2, many areas of everwet rainforest remained. Stuijts (1993) and Newsome & Flenley (1988) found no evidence of increased seasonality in their pollen cores (in the Barisan mountains and in West Java). It is probable that these areas had sufficient moisture to remain as rainforest because of their proximity to the continental shelf (therefore to the sea even at low sea levels, allowing convergent rainfall with moisture from the sea) and their altitude (allowing them to intercept the weak summer monsoon, fog and as they are cold, forcing precipitation). Northern Borneo probably also stayed everwet, for the same reason.

Around montane rainforest patches, lowland rainforest also probably survived. As explained above, the lowland areas probably received enough moisture (both directly from convergent rainfall from both the sea and from mountains, as well as gaining water from runoff from the mountains). The temperature in Southeast Asia at the LGM dropped by about 4°C (Morley 2000) bringing the altitudinal zones downhill by about 700 m (assuming a lapse rate of 0.6°C per 100 m increase in altitude). Lowland rainforest is typically found up to about 700-800 m (Richards 1996) so it is probable that (especially at the base of large mountains) lowland rainforest could continue through the LGM. It is likely that lowland forest migrated onto the newly exposed Sunda shelf, wherever possible (Morley 2000).

Table 5.1. Showing sites for which there is evidence for climate change in Southeast Asia

Site	**Period**	**Author**	**Change and evidence**
Bandung basin, W. Java, indicating local climate	80-10 Ka	Kaars & Dam (1995)	Palynological evidence for increased seasonality, reduced rainfall and colder temperatures (down to 7.2°C lower than now) and increased grassland.
Lombok ridge, indicating climate of northwestern Australia	300-244, 190-130, 38-12 Ka	Kaars (1991)	Palynological evidence of drier climates at these times, with increased grassland.
Subang airport, near Kuala Lumpur, Malay peninsula, indicating local climate	Mid-Pleistocene	Morley (2000)	Palynological evidence for a drier, grass-*Pinus* savannah system.
Peninsula Malaysia, the north coast of Java, Java sea	Late-Peistocene	Verstapen (1997)	Geological evidence indicates seasonal, savannah-like system
Southern and northern Sumatra, Sarawak	Pleistocene	Verstappen (1992)	Geological evidence indicates seasonal, savannah-like system.
Malay Peninsula and West Kalimantan	Oxygen Isotope stage 3	Thomas (2000)	Geological evidence indicates seasonal, savannah-like system.
Java	250Ka	Medway (1972)	Large fossil grazing herbivores, needing savannah vegetation to live.

Table 5.2. Showing sites for which there is evidence for continuing rainforest through the Quaternary.

Area of continuing forest	**Time**	**Author**	**Evidence for forest and amount of change.**
Sumatran highlands (1500 m a.s.l.)	31-13 Ka	Newsome & Flenley (1988)	Palynological evidence of montane forest migrating downhill during colder times.
Situ Bayongbong, W. Java (1300 m a.s.l.)	17-10 Ka	Suijts (1993)	Palynological evidence of montane forest migrating downhill.
Mentawai islands	Quaternary	Gathorne-Hardy & Harcourt-Smith in prep.	High rate of non-volant mammal endemism indicates continuous lowland rainforest.
Sarawak, Brunei and Sabah	Quaternary and before.	Ashton (1972, 1995), Morley (2000)	Inter riverian endemism of dipterocarps indicates continuous lowland rainforest.
Niah caves, Sarawak	40 Ka	Cranbrook (2000)	Fossils of *Presbytis* and *Pongo* indicate tall evergreen forest.
Punung caves, East Java	80-60 Ka	Bergh (1999)	Fossils of *Hylobates* and *Pongo* indicate lowland rainforest.
Mentawai islands, northern Sumatra, West Java and northern Borneo	80-10 Ka	Brandon-Jones (1998)	Present day primate distributions indicate lowland rainforest refugia.

5.2 Methods

Sampling sites

Termites had already been sampled using a standardised transect technique in Thailand (Davies 1997), Peninsula Malaysia (Jones & Brendell 1998), Sabah (Eggleton *et al.* 1997), Java and Way Kambas in Lampung, southern Sumatra (Gathorne-Hardy *et al.* 2000b), Jambi in central Sumatra, Tabalong in South Kalimantan (Jones, unpublished data) and northern Sumatra (Chapter 2).

In the summer of 2000 I sampled the termites of Siberut, Bukit Barisan National Park in Lampung, Barito Ulu in Central Kalimantan and Gunung Palung National Park in West Kalimantan. The sites were chosen so that in total, we had surveyed within all of the putative refugia, and non-refugia.

Sampling methods, identification and feeding group classification

I used the standardised transect sampling method to collect termites (see Chapter 1) and the termites collected were identified at the Natural History Museum (BMNH), London.

Environmental variables

Environmental data were collected for each transect. The following variables were analysed for their effect upon the termite composition.

Rainfall: mean annual rainfall measured in mm (from field station records or published records).

Altitude: Measured by an altimeter or from a map (25 m contours)

Disturbance: The level of disturbance was scored on a scale of 1-4:

1. Primary forest.

2. Old secondary/ regenerating closed canopy forest.

3. Young secondary/ regenerating forest with disturbed canopy.

4. Very badly disturbed forest.

Modern Island size: Island size at present sea levels. Thailand (north of the Kra ecotone) was taken to be part of the same ecological "island" as the Indian/ Burmese/ Indochinese forest area. Pasoh is south of the Kra ecotone, so the island size is approximately the same area as Peninsula Malaysia.

Log_{10} (modern island size).

Log_{10} (area of forest where the transect was run): estimated from vegetation maps or taken from site descriptions.

Log_{10} (distance to forest edge): The distance from each transect to the edge of the forest.

Data Analysis

All data are expressed as numbers of encounters (hits) per taxonomic unit per transect. The number of hits acts as a surrogate for abundance (Gathorne-Hardy *et al.* 2001, chapter 3).

I analysed the data at a functional taxonomic group level in order to minimise the effects of possible alpha-taxonomic mistakes and species patchiness. Though the

Table 5.3 Showing study sites and environmental variables

Site	Code	Site description	Long (decimal)	Lat (decimal)	Disturbance	Log10 modern island size	Modern Island Size (Km2)	Altitude (m)	Rainfall (mm)	Lg10 (Area)	Lg10 (Edge)
Thailand, Khao Sok	ThKhSo	Secondary evergreen rainforest	98.00	8.90	3	6.2886	1943645	500	1700	3.1764	3.080
Thailand Doi Sutep-Pui National Park	ThDoSuFP	Fire-protected dry deciduous dipterocarp forest	100.00	18.80	3	6.2886	1943645	575	1100	3.1764	3.080
Thailand Doi Sutep-Pui National Park	ThDoSuB	Burnt dry deciduous dipterocarp forest	100.00	18.80	3	6.2886	1943645	480	1100	3.1764	3.080
Thailand, Khao Yai National Park	ThKhYa	Primary evergreen rainforest	101.37	14.33	1	6.2886	1943645	780	4000	3.1764	3.080
Peninsula Malaysia, Pasoh Forest Reserve	PMPas1	Primary evergreen rainforest	102.3	2.98	1	5.1182	131286	100	2000	2.4786	2.904
Sabah, Danum Valley Conservation Area	SaDanOS1	Old logged (18 ya) evergreen forest	117.8	4.97	3	5.8711	743247	50	2700	3.0004	3.301
Sabah, Danum Valley Conservation Area	SaDanPF1	Primary evergreen rainforest	117.8	4.97	1	5.8711	743247	50	2700	3.0004	3.301
Central Kalimantan, Barito Ulu Research Station	BU1ry	Primary evergreen rainforest	116.93	0.1	1	5.8711	743247	150	3800	4	3.301
Central Kalimantan, Barito Ulu Research Station	BU2ndry	Old secondary evergreen forest (57 ya)	116.93	0.1	2	5.8711	743247	150	3800	4	2.699
West Kalimantan, Gunung Palung National Park	GP	Primary evergreen rainforest	110.12	-1.22	1	5.8711	743247	50	4300	2.954	4.255
South Kalimantan, Tabalong Logging Concession	Tabysf	Young Logged (2ya) evergreen forest	115	-2	4	5.8711	743247	450	3000	2.954	4.255
South Kalimantan, Tabalong Logging Concession	Tabosf	Old logged (15 ya) evergreen forest	115	-2	3	5.8711	743247	630	3000	2.954	4.255
Sumatra, Leuser Ecosystem, Ketambe Field station	SuKet500	Primary evergreen rainforest	97.65	3.68	1	5.62697	423611	500	3125	3.9543	3.477
Sumatra, Leuser Ecosystem, Suaq Belimbing Field station	SuSuaq	Primary evergreen rainforest	97.65	3.05	1	5.62697	423611	125	3231	3.9543	3.477
Sumatra, Leuser Ecosystem,MRT logging concession	SuMRT	Primary evergreen rainforest	97	3.18	1	5.62697	423611	200	3231	3.9543	3.001
Sumatra, Leuser Ecosystem, Bukit Lawang	SuBuLaw1	Primary evergreen rainforest	98.12	3.53	1	5.62697	423611	350	4675	3.9543	3.3015
Sumatra, Leuser Ecosystem, Lokop	SuLokop	Primary evergreen rainforest	97.53	4.42	1	5.62697	423611	500	1700	3.9543	3.0009
Sumatra, Jambi province	SuJaPF	Primary evergreen rainforest	102.1	-1.08	1	5.62697	423611	76	3000	1.0414	2.7796
Sumatra, Jambi province	SuJaLogF	Young Logged (3ya) evergreen forest	102.1	-1.08	4	5.62697	423611	85	3000	1.041	1.324
Sumatra, Way Kambas National Park	SuWK	Primary evergreen rainforest	105.67	-4.67	3	5.62697	423611	20	2000	4.989	2
Sumatra, Bukit Barisan Selatan National Park	BBar	Primary evergreen rainforest	104.5	-5.8	1	5.62697	423611	200	3250	3.562	3
Siberut National Park	SibT1	Primary evergreen rainforest	98.98	-1.35	1	3.65128	4480	100	3320	3.279	3
Java, Ujung Kulon National Park	JaUjKuln	Primary evergreen rainforest	105.5	-6.83	1	5.10209	126500	200	3140	3.7782	3.0009
Java, Pangandaran Nature Reserve	JaPangl1	Old Secondary evergreen forest (70 ya)	109	-7.72	3	5.10209	126500	75	3196	0.778	3.115

transect method is an efficient way of sampling termites, only about 35% of the local species pool is sampled in any one transect (Jones & Eggleton 2000). This means that unless strong environmental factors are being investigated, pseudoturnover dampens the signal shown by the data. Therefore, analysis at functional taxonomic group level (which has very little pseudoturnover) is appropriate when examining subtle effects (as in this chapter). Where two transects had been run at one site I amalgamated them and took the means of the number of encounters.

As almost all termite functional taxonomic groups were found in every site, it was appropriate to use linear response models to analyse the data. Because the process of standardising species data causes rare species to influence the analysis artefactually strongly (Jongman *et al.* 1995) I downweighted the two rarest functional taxonomic groups, the Kalotermitidae and the Apicotermitinae (both <3 hits transect^{-1})

As the effects of altitude are well known, and they are known not to correspond directly to height a.s.l. (chapter 3) I removed all non-lowland (>800 m a.s.l.) sites from the analysis.

I first ran an RDA, analysing those sites for which there is evidence for savannah in the LGM (Java, Way Kambas near Palembang, Gunung Palung in West Kalimantan and Pasoh near to Subang) and those for which there is evidence of refugia (Lokop, MRT, Bukit Lawang, and Suaq in northern Sumatra, Siberut and Danum in Sabah (see tables 5.1 and 5.2). As forward selection in the RDA showed that no measured environmental variable was significant we ran a principal

components analysis (PCA) of these sites and plotted the resulting ordination diagram.

I then added the other lowland sites to the matrix and again used an RDA to assess the importance of the environmental variables. Again, no environmental variable was significant. I therefore ran another PCA of the combined data to see where they fell in the final ordination diagram.

5.3 Results

In all 187 species of termite have been collected in transects in Southeast Asia. Of these 57 are not yet formally described (Gathorne-Hardy unpublished data). These morphospecies tend to be rare, often only collected once and frequently missing one of the castes, so a full description is often impossible.

No endemic species was found on Siberut. Most species are found in most parts of the region, as are functional taxonomic units and clades (Table 5.4).

The ordination diagram from the PCA of putative refugia and savannah sites (Fig. 5.1) showed that the putative savannah sites clump together (filled circles) and the refugia sites lie in a different area (open circles). When refugium is added to the matrix as an environmental variable, it is significant (P = 0.003).

Table 5.4. Showing the No. hits transect^{-1} of functional taxonomic groups

Site	Kalotermitidae	Rhinotermitidae	Macrotermitinae	*Foraminitermes* group	*Amitermes* group	*Termes/Capriterm es* group	Apicotermitinae	Group II Nasutitermitinae	Group III Nasutitermitinae
ThKhSo	2	4	13	0	5	6	0	14	0
ThDoSuFP	0	1	11	0	16	4	6	0	0
ThDoSuB	0	0	17	0	11	5	5	1	0
ThKhYa	1	5	17	0	2	10	0	6	1
PMPas1	0	7	34	1	3	15	1	4	4
SaDanOS1	1	13	13.5	0.5	13	31	0	8.5	3
SaDanPF1	0.5	8	9	1.5	14.5	40	1	5.5	5
BU1ry	0	23	8	0	5	28	0	17	12
BU2ndry	0	15	11	5	6	20	0	19	11
GP	0	7	3	1	6	14	0	0	0
Tabysf	0	16	24	0	19	32	0	11	3
Tabosf	0	9	15	0	16	33	2	1	1
SuKet500	0	4	12	0	0	7	0	26	7
SuSuaq	0	17	16	2	10	32	0	19	11
SuMRT	0	13	16	0	15	20	0	15	10
SuBuLaw1	0.5	13.5	3.5	3.5	15.5	23	0	29.5	6.5
SuLokop	2	11	3	1	9	25	0	41	9
SuJaPF	0	10	11	0	14	53	0	12	6
SuJaLogF	0	9	9	0	19	39	0	1	10
SuWK	0	3	4	0	3	11	2	12	0
Bbar	0	7	28	0	10	45	0	26	3
SibT1	0	5	3	0	2	42	0	20.5	12.5
JaUjKuIn	0	4	38	0	0	8	1	2	3
JaPangI1	0.5	0.5	20.5	0	1	3	0	6.5	0

When the other (unknown refugium status) sites were added to the data matrix, the ordination diagram of the PCA (Fig. 2) showed that the Thai sites seemed

to cluster with the putative savannah sites and Tabalong, Barito Ulu, Bukit Barisan and Jambi sites seemed to cluster with the putative refugia sites.

Fig 5.1. Ordination diagram showing PCA of functional taxonomic groups of termites from putative refugia and non-refugia. Filled circles are putative non-refugia, open circles putative refugia. Kalo= Kalotermitidae, Rhino= Rhinotermitidae, Macro= Macrotermitinae, Ami= *Amitermes* group, Foramin= *Foraminitermes* group, Apico= Apicotermitinae, Capri= *Termes/Capritermes* group, Nasuti2= GroupII Nasutitermitinae,
Nasuti3= Group III Nasutitermitinae.

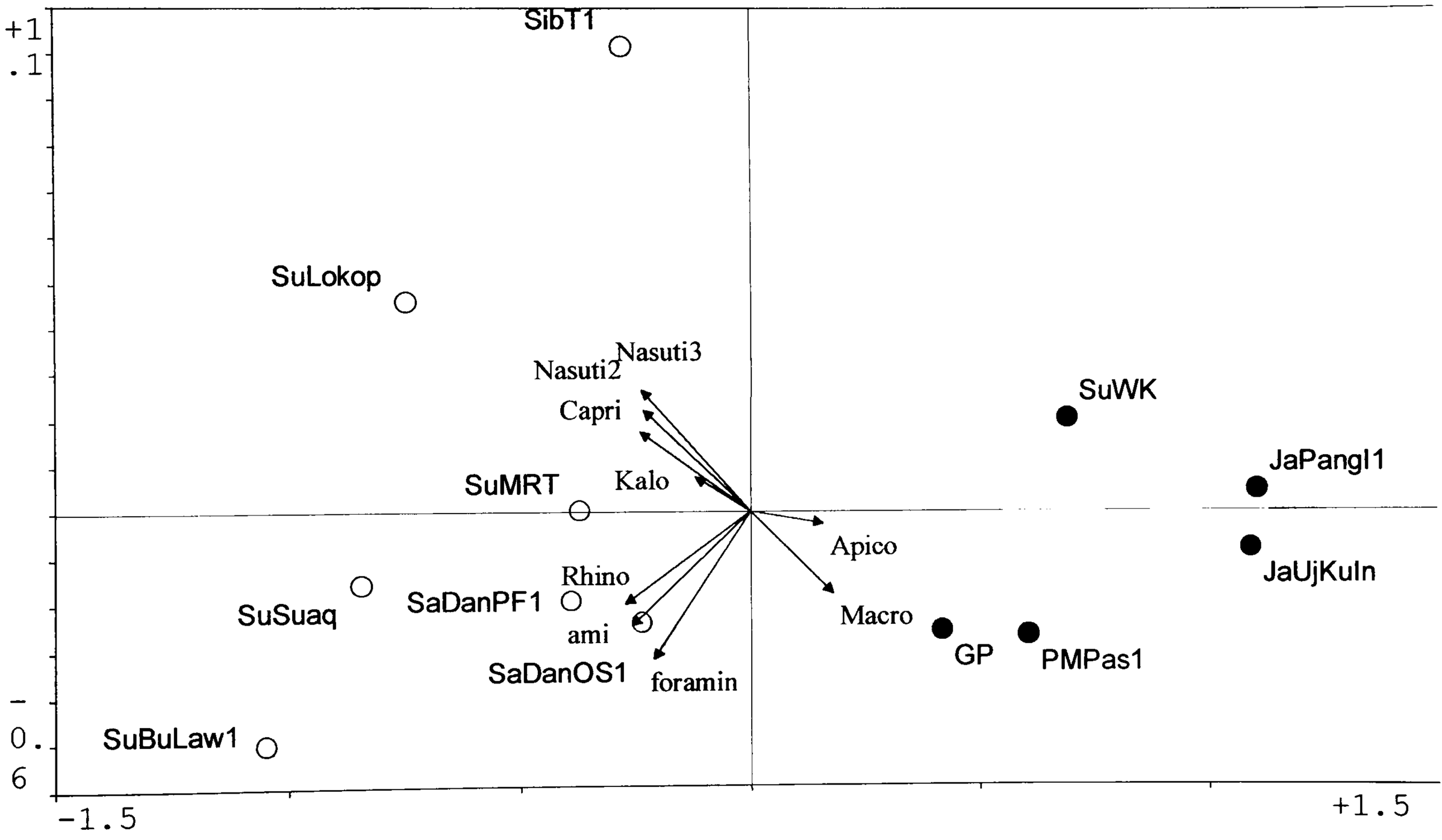
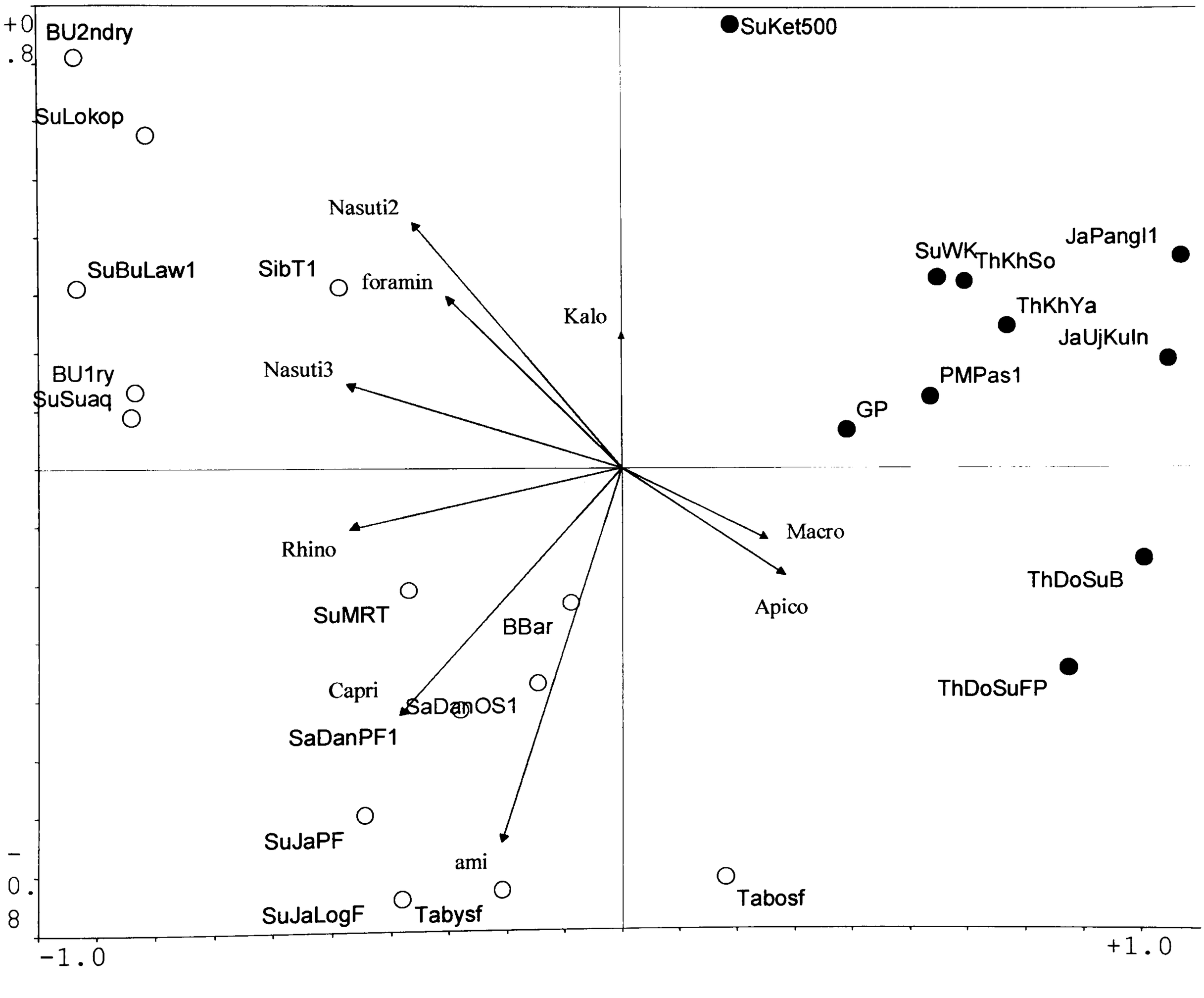
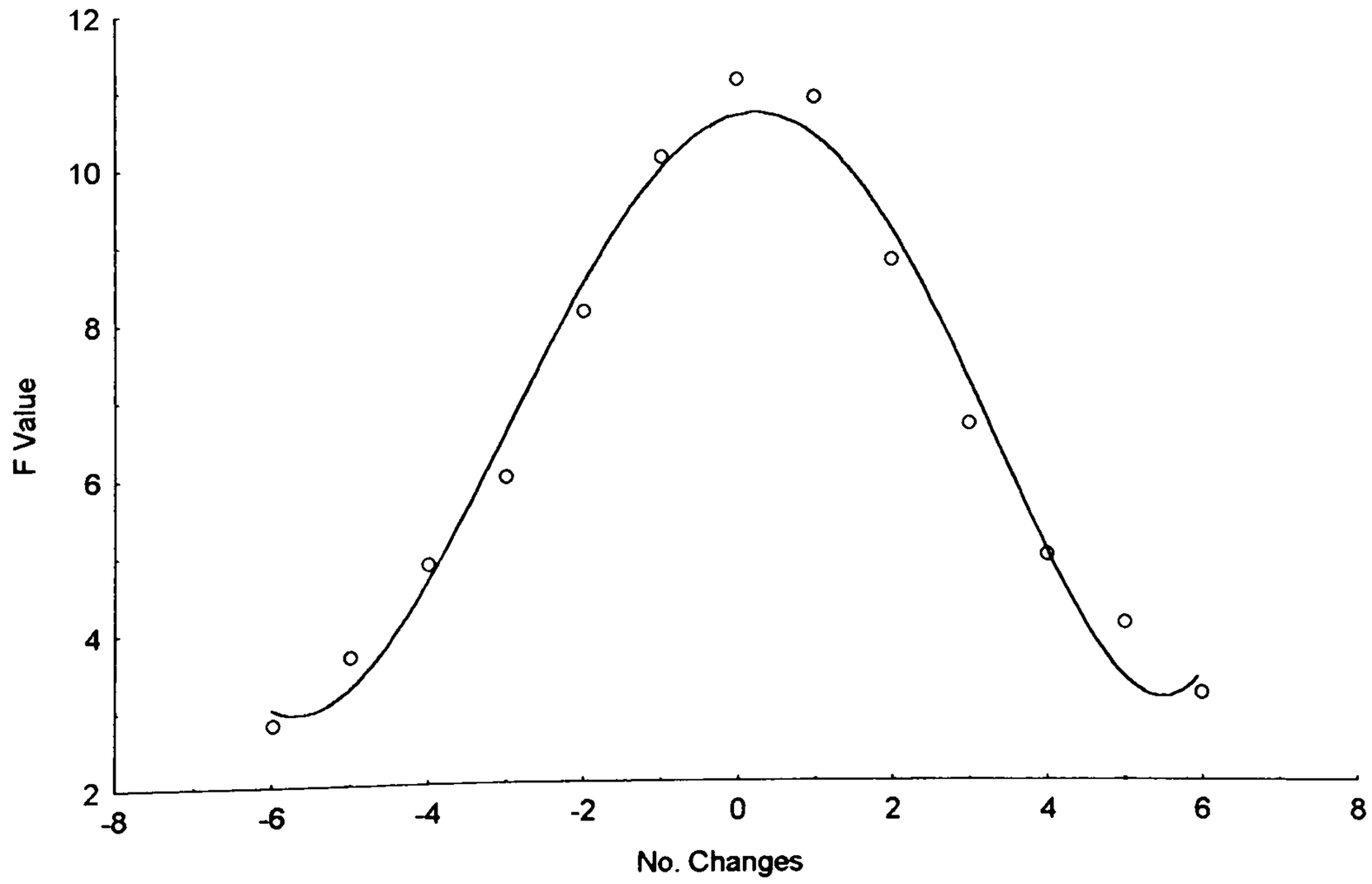


Fig 5.2. Ordination diagram showing PCA of functional taxonomic groups of termites from all sites. Filled circles are putative non-refugia, open circles putative refugia. Kalo= Kalotermitidae, Rhino= Rhinotermitidae, Macro= Macrotermitinae, Ami= *Amitermes* group, Foramin= *Foraminitermes* group, Apico= Apicotermitinae, Capri= *Termes/Capritermes* group, Nasuti2= GroupII Nasutitermitinae, Nasuti3= Group III Nasutitermitinae.



I tested to see whether sites formed separate clumps due to their refugium status by coding refugium as an environmental variable (coding sites that clustered close to putative refugia as refugia in the partial PCA and those close to putative savannah as savannah). I then changed the coding of one site, so that a proposed refugium site was coded as a savannah site, ran an RDA and forward selection provided me with an F value for refugium. I then changed the coding of another site, this time a proposed savannah site. Again we ran an RDA and extracted the F value. This continued until refugium status was no longer a significant environmental variable. The resulting F values from the RDA analysis were plotted and formed a bell-curve, with no changes of refugium status having the highest value, demonstrating that the perceived difference in the two clusters is real.

Fig. 5.3. Bell curve showing F-value against number of changes in refugium status. Showing that when there are no changes, the F-value is highest.



Macrotermitinae are found in all sites but are more abundant in savannah sites. Soil-feeding termites are also found in all sites but are more abundant in refugia sites (Fig. 5.2).

5.4 Discussion

Historical factors revealed

The PCA in Fig. 5.2 shows that the putative savannah sites have a different termite composition from the refugia sites. No modern environmental variable is significant, and I have demonstrated that the separation of the refugia and savannah sites is statistically significant. Therefore it is probable that termite composition can reflect history and is different in prehistoric savannah sites from prehistoric refugia.

I propose that the unknown refugium status sites which cluster around known savannah sites probably were savannah during the LGM, and that those which cluster around refugia were also refugia during the LGM.

Although my findings are indications only, and need additional palynological and geological work to provide confirmation, we have now a broader-based picture of the effects of glacial climate change on the rainforests of South East Asia.

During the ice ages, when the climate became more seasonal, rainforest refugia existed in the Mentawai islands, most of the north of Sumatra and at the base of the Barisan mountains. Northern Sarawak, Brunei, Sabah and eastern Kalimantan up to the Barito river were also refugia.

Thailand, the Malay Peninsula, south-east Sumatra, western Borneo (west of the Barito and the Lupar rivers) and Java were severely affected by Pleistocene drought. These areas were probably all vegetated by savannah or wooded (with *Pinus* or deciduous trees) savannah (Medway 1972, Cranbrook 2000, Morley 2000). The savannah probably spread out onto most of the exposed Sunda shelf.

Most termite species are found both in refuge and savannah areas (Tho 1992). It is therefore probable that small, local refugia (such as sheltered riverbanks etc.) existed throughout the region. The large river valleys of the exposed shelf were probably wet enough to provide an environment suitable for rainforest organisms.

I have used a combination of all works on the Pleistocene in Southeast Asia to draw a map, illustrating the possible extent of glacial rainforest contraction during the LGM.

Exception to the model

The Ketambe 500m site, though geographically in the middle of the northern Sumatran refugium, clumps together with the savannah sites in the second ordination diagram. It is thought that the Alas valley was dammed by volcanic debris from the Toba eruption of 74 Ka, forming a lake. The water level slowly decreased as the dam was eroded, and it is thought that the Ketambe 500m site was exposed about 10 Ka ago (van Schaik & Mirmanto 1985). It is interesting to note that though it was not a savannah, but was flooded, Ketambe shows a similar termite composition to the Pleistocene savannah sites.

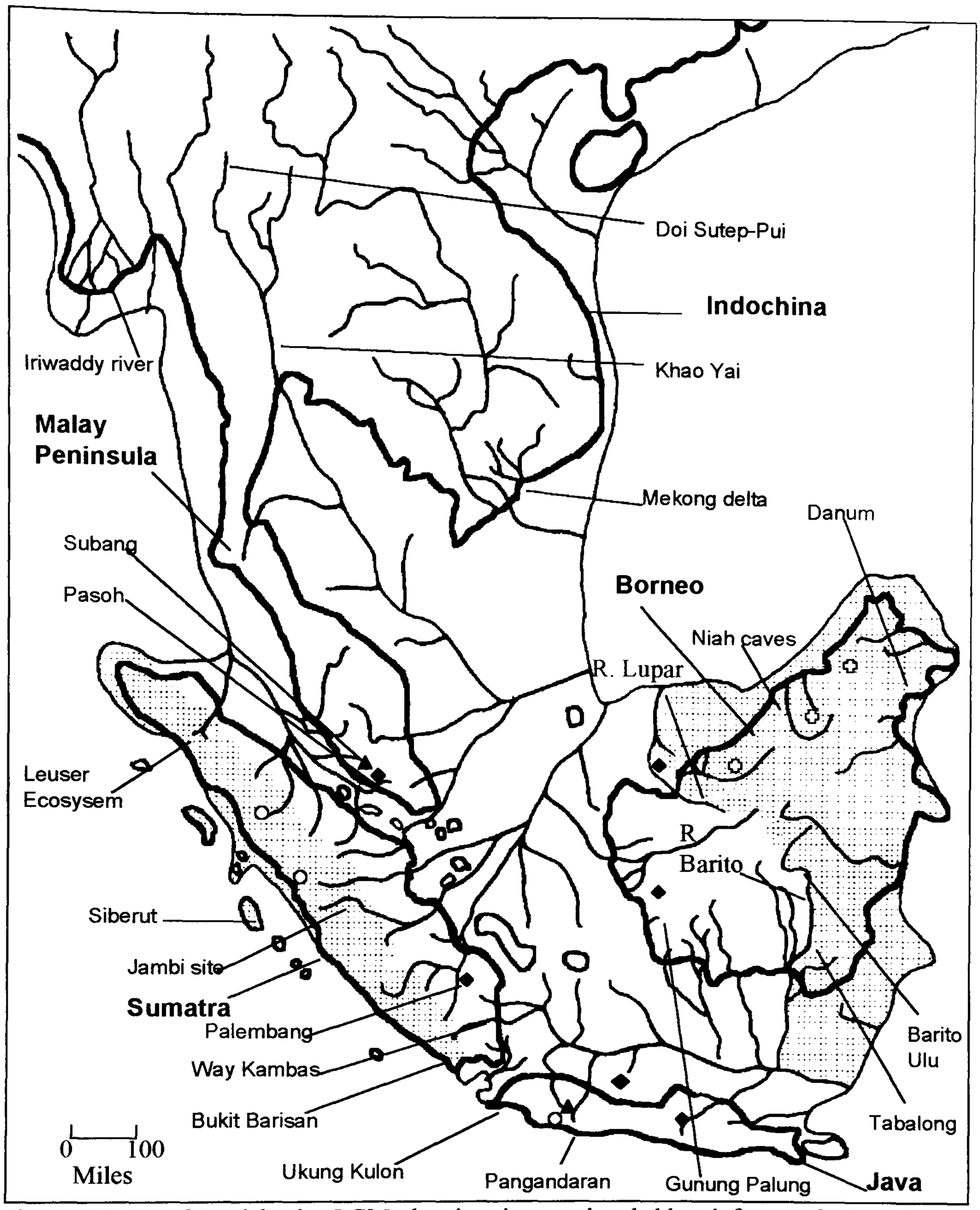


Figure 5.4 Map of Sundaland at LGM, showing rivers and probable rainforest refugia and savannah areas.

Heavy lines = Modern coastline

Light lines = Coastline at 120 m below present sea level
Modern and palaeo- river courses (from Voris 2000)

Stippled area =Probable rainforest refugia during LGM (limits are uncertain).

White area = Savannah areas during LGM (Limits are uncertain and river valleys were probably forested)

Termite sampling sites marked.

▲ = Palynological evidence indicating savannah during LGM

◆ = Geological evidence indicating savannah during the Pleistocene

○ = Palynological evidence indicating continuing rainforest

⬡ = Interriverian dipterocarp endemism indicating continuing rainforest

Feeding group composition: a comparison between refugia and non-refugia

The soil feeding termites of the *Termes/Capritermes* group and the soil-feeding Nasutitermitinae are more abundant (both as species richness and relative abundance) in refugia than non-refugia. Soil-feeding termites are most sensitive to disturbance (Eggleton *et al.* in press) and are the least efficient of termite colonisers (Gathorne-Hardy *et al.* 2000b). It is therefore to be expected that they should have a higher abundance in refugia sites.

It is known that group IV termites raise soil quality as a result of it passing through the gut (Donovan *et al.* 2001b). It is thought that group III feeders have a similar, though reduced effect, as they feed higher up the humification gradient (Donovan pers. comm.). The higher abundance and number of species of soil-feeding termites in refugia may therefore have significant effects on the soil quality.

Turnover across the refugia.

Most species are found in most areas and even in Siberut, local endemism is absent. It appears that the termites of Sundaland are quite homogenous, that species turnover is low across the region.

I tested the null hypothesis that species turnover (and therefore geographical position) has no significant effect on the composition of the termites of Sundaland. As termites still show a pattern from the effects of the climate change in the Quaternary, I used data only from Quaternary refugia. I used transect data from six primary lowland rainforest sites, from Sumatra (the Leuser Ecosystem, Aceh, Jambi and Bukit

Barisan National Park, Lampung), Siberut and Borneo (Danum Valley Conservation Area, Sabah and Barito Ulu Research Station, Central Kalimantan). The study sites are widely separated (between 500 and 2000 km from each other) so if the null hypothesis is correct, spatial variables should not significantly affect the termite composition.

I used canonical correspondence analysis (CCA) to analyse the data, following the method in ter Braak & Smilauer (1998). I used CCA to test whether spatial variables (latitude, longitude, longitude x latitude, longitude^2, longitude^3, longitude^2 x latitude, latitude^2, latitude^3 and latitude^2 x longitude, following Bocard *et al.* (1992)) could explain the differences between the sites. I also included environmental variables that are known to affect termites (altitude and rainfall). If either of these environmental variables significantly affected the termite composition, it was partialled out as a covariable.

Because I was testing the significance of spatial position, the actual position of the site where a transect is run becomes an important factor. If five transects were run close to each other, and one run far away, the geographical position shared by the five close transects would have effectively received five times more collecting effort than the site with one transect. Therefore, if transects were run within 200 km of each other (such as the five in the Leuser ecosystem) one transect was chosen at random from that area.

A Monte-Carlo permutation test showed that no spatial variable was significant in explaining the variation in composition across the region. As turnover (spatial factors) cannot explain the differences in termite composition, all differences

between sites are due to environmental factors. The termite fauna of Sundaland (all other environmental factors being equal) is homogenous throughout the region.

That there is no turnover across the Sunda region means that the termite fauna of different sites with different treatments can be compared with one another without having to take the site's position into consideration. This is particularly useful when examining the effects of different types of disturbance, as it is rare to find several types of disturbance in one area (see chapter 6).

No genus of termite is endemic to Sulawesi (Chapter 2) and no species endemic to Siberut (above). Termites in general are poor dispersers (Chapter 2, Gathorne-Hardy *et al.* 2000), and we have now found that their composition is homogenous across the Sunda region. This strongly indicates that termites are extremely slow to evolve new species.

The reason that termites evolve so slowly is probably a result of their dependence on gut sybmionts (Archaea and Bacteria and Protazoa in the lower termites, and just Archaea and Bacteria in the higher termites), to change their food into a form suitable for the termites to be able to digest. Any change in the termite's feeding patterns has to be tracked by a corresponding change in those of the symbionts (Davies 2001).

Soldier and worker termites may evolve at different rates. Within a genus (and often a functional taxonomic group) the soldiers are much more variable than the workers. It is generally impossible to identify a specimen to species if it is a worker, but often possible if it is a soldier. Changes in soldier morphology are constrained only by function (whether it is still an effective soldier) and the amount of inherent

genetic variation available. They are therefore able to change faster than workers, which are constrained by their gut symbionts.

The refugia in context, a regional history.

It is probable that Southeast Asia has been populated by termites since the late Cretaceous or early Paleocene, for Kalotermitidae and Rhinotermitidae are extremely good colonisers (Gathorne-Hardy *et al.* 2000b) and are not rainforest dependant. Most of the Southeast Asian soil feeding termites (the *Termes/Capritermes* group, *Labritermes* and the Apicotermitinae) are thought to be descended from Gondwanic ancestors, and probably rafted from Africa on the Indian plate (Eggleton 2000, Davies 2001). The soil-feeding Nasutitermitinae probably evolved from wood-feeding nasutes, which had rafted and island-hopped over the Pacific from South America (Davies 2001, Eggleton & Davies in press).

It appears that the first land connection between India and Asia appeared in the Oligocene (Najman *et al.* 2001). This, coupled with a perhumid lowland climate in Burma and Assam allowed Gondwanic rainforest organisms to colonise mainland Asia (Morley 2000). Rainforest was rare in Southeast Asia during the Oligocene and Early Miocene, as the climate was predominantly seasonal and dry. The climate changed to a perhumid one in the Mid-Miocene, and rainforest colonised the region (Morley 2000). Termites probably followed the forest to Southeast Asia and colonised all forested areas. From the early until the late Miocene Southeast Asia was effectively a single lowland (apart from the Bornean highlands) land mass (Hall 1998). The region remained as a single rainforested block until the late Miocene-early

Pliocene (Muller 1972, Morley 2000). A few periods of heightened Gramineae pollen have been found, but not enough to indicate a large area of Savannah (Muller 1972).

Speciation of soil-feeding termites is thought to require a large area of lowland rainforest that is stable for a long time (Davies 2001). These requirements were met during the Miocene in Southeast Asia when they applied for between 10 and 15 Ma. It is probable that the endemic Southeast Asian soil-feeding termites (both the Termitinae and the Nasutitermitinae) speciated during the Miocene.

Uplift of the Tibetan plateau and the Himalayas in the late Miocene, early Pliocene strengthened the monsoon system (An 2000, Ruddiman & Kutzbach 1990). This probably increased seasonality in Indochina and Java (there is evidence of savannah vegetation from Mio-Pliocene deposits in the Iriwaddy delta and Pliocene Java (Morley 2000)), reducing the size of the rainforest block.

With the advent of Quaternary glaciations, savannah formed in large parts of Southeast Asia, driving rainforest obligates to the refugia identified above. The large rivers draining the Sunda shelf probably provided refugia along their banks too. Savannah organisms, such as mastodons, stegodonts, elephants, antelopes, hippopotami and oxen proliferated, as did *Homo erectus* (Whitten *et al.* 1996, Cranbrook 2000). During interglacials, the sea rose, the rainforest returned and the savannah animals were constrained to Indochina and a few patches of Java. Each of the glacial episodes probably showed a similar pattern.

However, in the most recent glacial cycle, things had changed. By 40000 C^{14} BP *H. sapiens* had arrived in the region, bringing with him a hunting technology (including tame dogs) advanced enough to kill large mammals such as wild cattle

(Cranbrook 2000). The large, savannah mammals (and their predators: the sabre-toothed cat and hyenas) did not survive into the Holocene. There is no evidence that the LGM was any more severe than other glaciations (Petit *et al.* 1999), so it appears likely that human overhunting was responsible for their extinctions, as it was in America and Australia (Ward 1997, Whitten *et al.* 1996). These may have been the first of a series of human-induced extinctions in the region.

It is probable that the rainforest refugia are centres of speciation, not because of their fragmentation and subsequent isolation from each other, but because of their long-term stability, allowing fragile organisms (such as soil-feeding termites) to persist. The recognition of the refugia sites, and that recovery from prehistoric disturbance is still not complete, highlights the long-term fragility of the rainforest ecosystem and the importance of conserving prehistoric refugia as modern rainforest refugia.

Chapter 6. The effects of human disturbance on the termites of Sundaland.

A version of this chapter is in press as: Gathorne-Hardy F.J, D.T. Jones and Syaukani. A regional perspective on the effects of human disturbance on the termites of Sundaland. In *Biodiversity and Conservation.*

6.1 Introduction

The Sundan rainforests have a history of fragmentation; increased seasonality during glacial times caused the core of the region to become savannah-like, with rainforest only found in a few refugia at the edges of the region (Chapter 5). In the present climatic optimum (the past *c.* 10,000 years; the Holocene) rainforest has recolonised almost all of the area and, with the exception of Java (Whitten *et al.* 1996), was not extensively disturbed until the 1950s (Whitmore 1984). Since then, however, the area has suffered huge amounts of disturbance. Myers *et al.* (2000) estimated that only 7.8% of Sundaland's primary forest remains. Widespread fires in 1982-3 destroyed at least 2.5 million ha in Borneo (Taylor *et al.* 1999), and in 1997-8 destroyed over 8 million ha of forest in Sumatra and Borneo (Whitmore 1999). Illegal logging is penetrating deep into the Indonesian National Parks and protected areas (Sunderlin 1999, van Schaik *et al.* 2001).

Legal logging practices vary throughout the region, but in general only the large, commercially valuable trees are removed. Most of the damage to the forest is collateral,

caused by falling trees and extraction of the timber. Estimates of damage caused by logging vary from 50% to 85% of the forest area (MacKinnon *et al.* 1997, Cannon *et al.* 1998). Logged forests are not clear felled and a logged area usually consists of a mosaic of highly disturbed, slightly disturbed and undisturbed areas (MacKinnon *et al.* 1997). Logging changes the forest community, often altering tree species composition and reducing the diversity of mammals and birds (MacKinnon *et al.* 1997). Forest communities can recover from selective logging, especially if it is carefully managed (Richards 1996, Cannon *et al.* 1998, Whitmore 1999).

Figure 6.1 A red *meranti* felled to make a canoe in Siberut. Note the broken trunks at the top of the picture.

However, one of the side-effects of logging is that it opens up the land to human encroachment, providing access roads and partially cleared land. Therefore, in many logged areas, farmers settle and practice slash-and-burn agriculture (MacKinnon *et al.* 1997). Slash-and-burn agriculture (otherwise known as swidden or shifting cultivation, or *ladang* in Indonesia and Malaysia) has been practised in the region for at least 4000 years (Cranbrook 2000). Typically, an area of forest (either primary or secondary) is felled (though useful fruit trees are allowed to remain), the wood and debris are left for a month or two to dry and is then burned. Large logs and tree stumps are usually only incompletely burned and remain on the field. Rice, cassava, maize and other crops are then planted. The fields tend to be used for only a year or two until high weed density and lowered soil fertility leads the farmers to abandon them. The fields are generally left fallow for about 10-20 years (Chin 1985, MacKinnon *et al.* 1997, Gönner 2000). Trees such as rubber or fruit trees are sometimes planted in the fallow areas (Lawrence *et al.* 1998, Gönner 2000). If the land is recultivated and reburned too often, fire-tolerant species such as *Imperata cylindrica* may become dominant, often slowing natural re-aforestation (Whitten *et al.* 1984).

Shifting cultivation has been blamed as the primary agent of rainforest loss (Myers 1993) and clearance of forest for agriculture certainly has a far greater impact on forest structure and communities than logging (Whitmore 1984, Richards 1996). However, opening *ladang* removes less primary forest than either logging or conversion to oil-palm plantations (Lawrence *et al.* 1998).

With the recent increase in primary rainforest destruction and the associated increase in habitat fragmentation and degradation, there is great concern that the region

will lose its forests and biodiversity forever (Richards 1996). At the present rate of uncontrolled logging, Sumatra is predicted to lose all of its lowland primary forest by 2005, and Kalimantan by 2010 (Jepson *et al.* 2001).

Figure 6.2 Land cleared and burned off for oil palm plantation. Near Sinkil, Sumatra

Termites

The termite fauna of Sundaland is relatively depauperate in species and biomass, and energy flow is low, when compared with the Afrotropics (Eggleton *et al.* 1999). However, they are still the most important arthropod decomposers in the lowland Sundan rainforests (Collins 1983, 1989) and are directly or indirectly responsible for a large part of the region's decomposition, soil movement and organic matter translocation (Matsumoto and Abe 1979, Abe 1980, Collins 1989, Jones 1996). Sundan termite

production has been estimated at about 300kg ha^{-1} yr^{-1} and they provide a valuable food source for ants, birds, orang-utans, pangolins and other animals (Collins 1989).

Termites are thought to play an essential role in the recovery of soil fertility after habitat disturbance (Davies *et al.* 1999). They are known to be sensitive to disturbance, especially to forest canopy loss (Dibog *et al.* 1999, Eggleton *et al.* 1996, 1997, 2001, Gathorne-Hardy *et al.* 2001). Before forest management and conversion decisions are made, it is important to have an understanding the effects on termites of different types disturbance. In this chapter I investigate the effects of different types of disturbance (from selective logging to complete clearance for cassava fields) on termite composition. I also assess the recovery of the termite fauna from different disturbance effects.

6.2 Methods

Termites have been sampled from throughout the Sunda region, using the standardised transect sampling protocol. Transects have been run in both primary forest and disturbed areas. I compared termites from areas that had suffered disturbance with those of primary, undisturbed forest in order to assess the effects of disturbance on termites.

Sampling sites

Termite assemblages have been shown to have been affected by climate change during the Quaternary, when large areas of Sundaland were savannah (chapter 5).

Because the savannah ecosystem had little canopy cover, and termites are known to be

sensitive to forest canopy loss (Dibog *et al.* 1999), I have only used termite data from sites that are thought to have been Quaternary rainforest refugia.

I used transect data from the following sites in Borneo and Sumatra: Danum Valley Conservation Area in Sabah, a logging concession in Tabalong district in South Kalimantan and Barito Ulu Research Station in Central Kalimantan, the Leuser Ecosystem in northern Sumatra, Jambi, Siberut National Park and Bukit Barisan National Park, Lampung (See map in chapter 5)(Eggleton *et al.* 1997, Jones & Prasetyo in press, Gathorne-Hardy *et al.* 2001, in press). The sampling was carried out in sites with different local levels of disturbance (Table 1).

Sampling method and identification

Termites were sampled using the standardised transect method (Davies 1997, Jones and Eggleton 2000, Chapter 1). The specimens were then identified at the Natural History Museum (BMNH), London.

Environmental variables

I scored disturbance as a series of seven different nominal variables, depending on the type of disturbance and the age since the disturbance had taken place. The categories are as follows: A. Primary forest, B. Old secondary (forest completely cleared, 57 years old) regenerating closed canopy forest, C. Logged (15-18 years old)/ regenerating forest with disturbed canopy, D. Logged (2-3 years old)/ regenerating forest with highly disturbed canopy, E. Natural forest with crop trees added, F. Silviculture/ plantation monoculture and G. Cassava field, *Imperata* grassland.

Other environmental data were collected and analysed for their possible effect on termites: Rainfall (mean annual rainfall measured in mm per year, from field station records or published records), Altitude (measured by an altimeter or from a map, 25 m contours), Island size and Log_{10} (island size).

Data analysis.

All termite data from transects are expressed as numbers of encounters (hits) per taxonomic unit, per transect. The number of hits acts as a surrogate for relative abundance (Gathorne-Hardy *et al.* 2001).

I analysed the termite data at the functional taxonomic group level, in order to minimise the effects of species patchiness (pseudoturnover) and any alpha-taxonomic mistakes. Analysis at this level maintains a high amount of taxonomic and functional information and has been found to be effective in elucidating patterns at a regional scale (chapter 5). Where two transects were run within 5 km of each other in the same forest disturbance category, they were amalgamated and means of the number of encounters were taken.

Site	Site description	Long (decimal)	Lat (decimal)	Disturbance	Island Size (Km^2)	Log10 island size	Altitude (m)	Rainfall (mm)
Sabah, Danum Valley Conservation Area	Old logged (18 ya) evergreen forest	117.8	4.97	C	743247	5.8711	50	2700
Sabah, Danum Valley Conservation Area	Primary evergreen rainforest	117.8	4.97	A	743247	5.8711	50	2700
Sabah, Danum Valley Conservation Area	Young Logged (3ya) evergreen forest	117.8	4.97	D	743247	5.8711	50	2700
Central Kalimantan, Barito Ulu Research Station	Primary evergreen rainforest	116.93	0.1	A	743247	5.8711	150	3800
Central Kalimantan, Barito Ulu Research Station	Old secondary evergreen forest (57 ya)	116.93	0.1	B	743247	5.8711	150	3800
South Kalimantan, Tabalong district	Young Logged (2ya) evergreen forest	115	-2	D	743247	5.8711	450	3000
South Kalimantan, Tabalong district	Old logged (15 ya) evergreen forest	115	-2	C	743247	5.8711	630	3000
South Kalimantan, Tabalong district	*Gmelina arborea* plantation	115	-2	F	743247	5.8711	810	3000
Sumatra, Leuser Ecosystem, Suaq Belimbing Field station	Primary evergreen rainforest	97.65	3.05	A	423611	5.62697	125	3231
Sumatra, Leuser Ecosystem, MRT logging concession	Primary evergreen rainforest	97	3.18	A	423611	5.62697	200	3231
Sumatra, Leuser Ecosystem, Bukit Lawang	Primary evergreen rainforest	98.12	3.53	A	423611	5.62697	350	4675
Sumatra, Leuser Ecosystem, Lokop	Primary evergreen rainforest	97.53	4.42	A	423611	5.62697	500	1700
Sumatra, Jambi province	Primary evergreen rainforest	102.1	-1.08	A	423611	5.62697	50	3000
Sumatra, Jambi province	Young Logged (3ya) evergreen forest	102.1	-1.08	D	423611	5.62697	50	3000
Sumatra, Jambi province	Jungle rubber (rubber and forest trees)	102.1	-1.08	E	423611	5.62697	50	3000
Sumatra, Jambi province	Rubber plantation	102.1	-1.08	F	423611	5.62697	50	3000
Sumatra, Jambi province	*Paraserianthes falcata* plantation	102.1	-1.08	F	423611	5.62697	50	3000
Sumatra, Jambi province	*Imperata*-covered land	102.1	-1.08	G	423611	5.62697	50	3000
Sumatra, Jambi province	Cassava field	102.1	-1.08	G	423611	5.62697	50	3000
Sumatra, Bukit Barisan Selatan National Park	Primary evergreen rainforest	104.5	-5.8	A	423611	5.62697	200	3250
Siberut National Park	Primary evergreen rainforest	98.98	-1.35	A	4480	3.65128	100	3320

Table 6.1 Showing study sites and environmental variables

I used multivariate ordination techniques to analyse the data. As almost all termite functional taxonomic groups were found in every site, it was appropriate to use linear response models to analyse the data. We therefore used Redundancy analysis (RDA) following the method in ter Braak and Smilauer (1998).

Although I have shown that for termites, turnover is low at species level across the region (Chapter 5), it was sensible to run a preliminary analysis to test whether functional taxonomic group turnover has a significant effect on the functional taxonomic group composition of termites in the study sites. Functional taxonomic group level analysis minimises the effects of pseudoturnover, which is high with species level analysis (Chapter 5) so it is possible that turnover across the region may have an effect on the termites at this taxonomic level.

I analysed all study sites with primary forest. I used RDA to test whether spatial variables (latitude, longitude, longitude x latitude, longitude^2, longitude^3, longitude^2 x latitude, latitude^2, latitude^3 and latitude^2 x longitude, following Bocard *et al.* (1992)) could explain the differences between these sites. A Monte-Carlo permutation test showed that no spatial variable was significant. The eigenvalue of the first axis of the RDA is short (0.279) and when evaluated with a Monte-Carlo permutation test it is not significant (P=0.166), showing that there is no measured statistical difference between the structure of the termite functional taxonomic groups of these sites. This demonstrates that the primary forest termites from our study sites have a homogenous composition (at the functional taxonomic group level) despite the fact that they are geographically distant (the Leuser ecosystem is 2000 km from Danum Valley). As the termite functional

taxonomic group composition has been demonstrated to be the same in all of our sites, I can compare sites directly without reference to the site's location.

I analysed disturbance as part of a matrix of all the environmental variables listed above, which allows us to see its effects in an ecological context. If a non-disturbance environmental variable had a significant effect on the termite composition, it was partialled out as a covariable.

I used a one way ANOVA to test whether the relative abundance of termites (the number of hits transect^{-1}) is affected by the different disturbance categories.

6.3 Results

In the forward selection of the RDA I found that modern island size had a significant (P = 0.037) effect on the termite functional taxonomic group composition. I partialled out this variable as a covariable. With island size partialled out, disturbance categories F (Silviculture/ plantation monoculture) and G. (cassava field, *Imperata* grassland) were the only environmental variables to affect termite functional taxonomic group composition significantly (Table 3 category F: P=0.001, G: P=0.006).

Table 6.2. Showing the termite functional taxonomic groups found in transects. Transects in italics are significantly affected by disturbance.

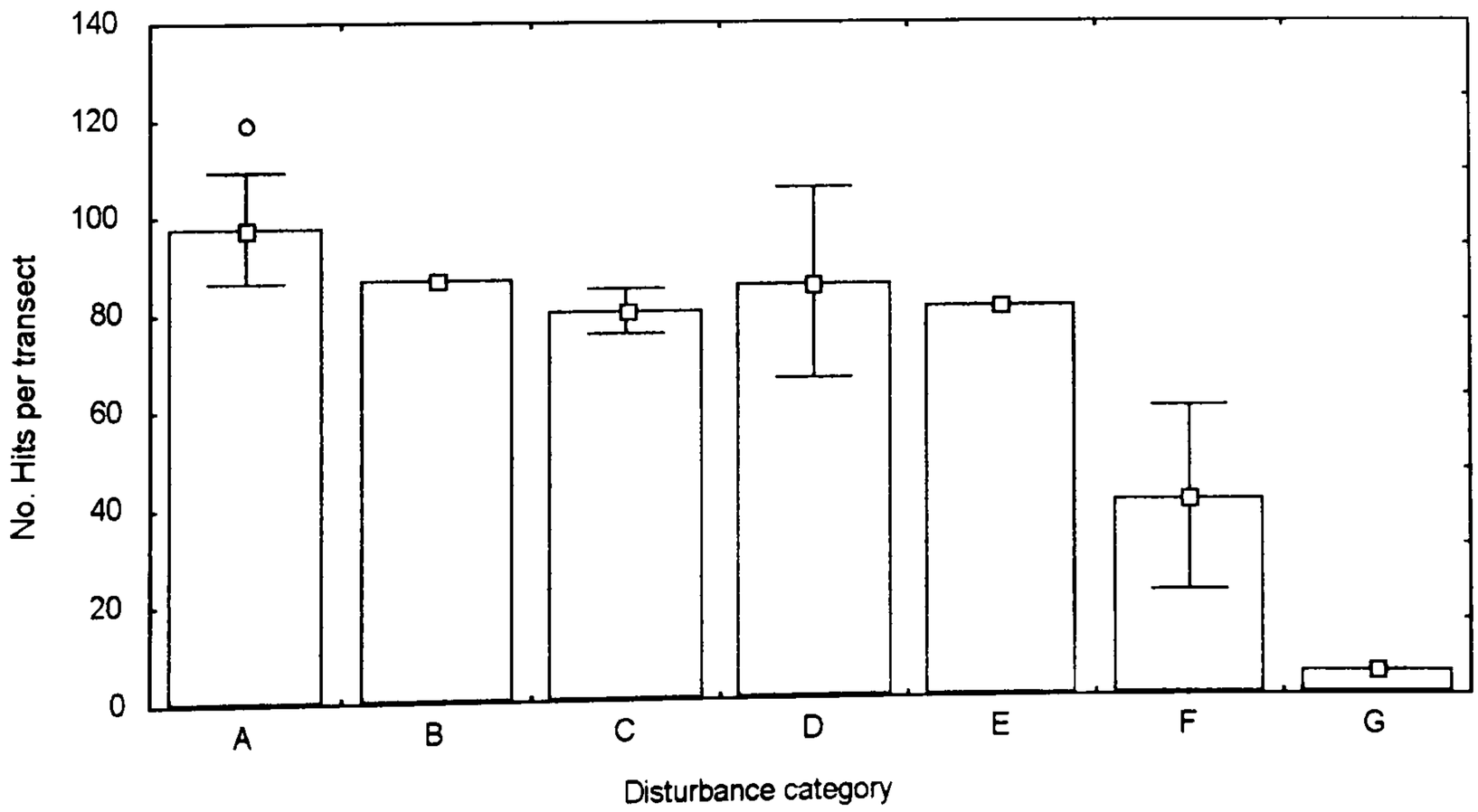
Site	Kalotermitidae	Rhinotermitidae	Macrotermitinae	*Foraminitermes* group	*Amitermes* group	*Termes*/ *Capritermes* group	Apicotermitinae	Group II Nasutitermitinae	Group III Nasutitermitinae	No. Hits per transect
Tabalong, Gmelina plantation	*0*	*17*	*7*	*0*	*0*	*0*	*0*	*1*	*0*	*25*
Jambi, Paraserianthes falcata plantation	*6*	*16*	*0*	*0*	*4*	*4*	*0*	*5*	*0*	*35*
Jambi, Imperata land	*0*	*0*	*0*	*0*	*4*	*5*	*0*	*0*	*0*	*9*
Jambi, Cassava field	*0*	*0*	*1*	*0*	*0*	*0*	*0*	*0*	*0*	*1*
Jambi, rubber plantation	*4*	*3*	*6*	*2*	*1*	*35*	*0*	*11*	*0*	*62*
Danum, young logged forest	0	11	8.5	0	3	22.5	3.5	13.5	3.5	65.5
Tabalong, young logged forest	0	16	24	0	19	32	0	11	3	105
Jambi, young logged forest	0	9	9	0	19	39	0	1	10	87
Danum, old logged forest	1	13	13.5	0.5	13	31	0	8.5	3	83.5
Tabalong, old logged forest	0	9	15	0	16	33	2	1	1	77
Jambi, jungle rubber	1	11	8	1	1	53	0	4	2	81
Barito Ulu, secondary forest	0	15	11	5	6	20	0	19	11	87
MRT primary forest	0	13	16	0	15	20	0	15	10	89
Danum, primary forest	0.5	8	9	1.5	14.5	40	1	5.5	5	85
Barito Ulu, primary forest	0	23	8	0	5	28	0	17	12	93
Suaq primary forest	0	17	16	2	10	32	0	19	11	107
Bukit Lawang Primary forest	0.5	13.5	3.5	3.5	15.5	23	0	29.5	6.5	95.5
Lokop, primary forest	2	11	3	1	9	25	0	41	9	101
Jambi, primary forest	0	10	11	0	14	53	0	12	6	106
Bukit Barisan, primary forest	0	7	28	0	10	45	0	26	3	119
Siberut, primary forest	0	5	3	0	2	42	0	20.5	12.5	85

Table 6.3. Showing conditional results of RDA of all environmental variables (with island size as a covariable). F and P values are derived from a Monte Carlo Permutation test.

Variable	P value	F value
Disturbance category G	0.006	3.30
Disturbance category F	0.001	4.56
Disturbance category B	0.337	1.17
Disturbance category A	0.146	1.57

The one-way ANOVA showed that the disturbance categories have a significant effect on the relative abundance of termites ($F_{(6,14)} = 16.6$, $P = <0.0001$). Figure 1 shows that sites in categories F and G have a lower relative abundance of termites than in other sites.

Figure 6.3. Graph showing the mean number of hits (with variances) of termites in the different disturbance categories



6.4 Discussion

Disturbance categories F and G have a significant effect of termite functional taxonomic group compositions, and the relative abundance in these sites is lower than in the others. This shows that if forest is removed and replaced with monoculture plantations the termite functional taxonomic group composition is significantly affected and relative abundance decreases. The other disturbance categories do not significantly affect termite functional taxonomic group composition or relative abundance.

Category G: Field, *Imperata* grassland.

The termites found in the cassava field and *Imperata* area are strongly affected by disturbance. The abundance is much lower (about 5% of the termite abundance found in not significantly disturbed sites), and only two FTGs are found. The absence of a canopy is known to dramatically reduce the diversity and abundance of termites, especially soil feeders (Dibog *et al.* 1999, Eggleton *et al.* in press, Jones and Prasetyo in press). I think that soil feeding termites, which are thought to live on an energetic knife edge (Dibog *et al.* 1998, Jones 2000, Davies 2001) are pushed to the lower limit of energetic viability due to the greater diurnal temperature and moisture fluctuations in opened forest. The lack of dead wood probably also has an effect, limiting the amount of food available to

wood feeders and, in the case of the lower termites, nesting sites (Jones and Prasetyo in press).

Category F: Silviculture/Plantation monoculture.

The plantation sites are also significantly affected by disturbance, with a lower relative abundance of termites than the not significantly disturbed sites, and a different functional taxonomic group composition. The plantation monocultures probably provide too little structural complexity and buffering against diurnal change to allow the termites to reach the diversity and abundance found in not significantly disturbed sites (Jones and Prasetyo in press).

Group III Nasutitermitinae are found in none of the significantly disturbed sites, while they are present in all the less disturbed sites and the primary forest (Table 4). Termites of this group are small-bodied, have small colonies and nest in loose, amorphous nests in the topsoil (personal observations). Group III Nasutitermitinae may be more vulnerable than others to the increased diurnal temperature and moisture fluctuations in highly disturbed areas because of these attributes.

Category E: Natural forest with crop trees added.

Only one site was sampled in this category, so my results are not conclusive. However, it appears that adding rubber trees to the forest has no significant effect on the termite functional taxonomic group composition and that the relative abundance of termites is similar to undisturbed forest.

Categories D and C: Logged forest.

Selective logging appears to have had no significant effect on termite FTG composition. The logged forest sites, though they have been disturbed, have not been clear-felled. They still maintain some canopy cover and undisturbed areas. They are usually also part of a mosaic of primary, recovering and recently logged forest. Therefore, as well as much of the original fauna remaining (Eggleton *et al.* 1999), a supply of recolonising termites is available to the recently disturbed, logged forest, enabling quicker recovery.

The logged sites surveyed have only been logged once, and were logged selectively. However, often sites in logging concessions are re-logged within 20 years from the first cut (MacKinnon *et al.* 1997), which causes further disturbance and opening of the canopy. These second cuts are often much less selective, taking even small (<40 cm DBH) trees (personal observations).

Illegal logging (often with government, police and military protection) has increased dramatically in the past few years, harvesting as many logs as the legal sector and often invading conservation areas (Sunderlin 1999, Jepson *et al.* 2001). Illegal loggers often take very small trees and can log areas left by commercial loggers. Helicopter extraction too, enables loggers to take trees from steep slopes, which had been left untouched until now (Putz *et al.* 2001). In the future it would be sensible to survey a site that has been more intensively logged than is current practice, to see how termites are affected by almost complete clearance. I hypothesise that intensive logging will have a significant effect on termites.

Category B: Old secondary regenerating forest.

Although I have sampled from only one site in this category, so my results are not conclusive, it appears that the forest termite community can recover fully (at the functional taxonomic group level) from severe disturbance. The Barito Ulu Secondary forest site is an area that was almost completely cleared for farming in 1943, and the remaining debris was burned. Charred wood can still be seen buried in the soil. The impact on termites was probably severe, with only a few species surviving (this has been observed on land cleared for farming in Sumatra (Syaukani, unpublished data)). The Barito Ulu site was then abandoned after a few years and high stature forest has developed. This site indicates that if a source of forest termites is close to a disturbed area (about 100m in this case), complete recovery is possible in a short time (*c.* 60 years), even after complete removal of the forest.

Though highly disturbed sites can be recolonised relatively quickly from nearby sources, over longer distances, recovery takes a much longer time. During Quaternary glaciations, increased seasonality caused much of Southeast Asia to be covered by savannah vegetation, with only a few rainforest refugia (Morley 2000, Gathorne-Hardy *et al.* in press, Figure 1). The absence of forest cover in the savannah areas probably had a similar effect to that caused by present day disturbance. The termite composition in former savannah sites has not yet recovered and is different from the refugia sites (Gathorne-Hardy *et al.* in press). Recolonisation over the 150 km (or more) from refugia sites to historical savannah areas (such as from Bukit Barisan to Way Kambas, Figure 1) has not been completed in the *c.* 10,000 years of the Holocene. Therefore, it is probable that if large areas of land (100s of km^2) are highly and uniformly disturbed (burned or

converted to large plantations), the termite composition of these areas will not recover for millennia even when forest cover returns.

Islands

Islands are at a special risk from large-scale disturbance. If the whole of an island is highly disturbed and most termites made locally extinct, recolonisation is likely to take a very long time, as most termites are very poor at crossing water gaps (Gathorne-Hardy *et al.* 2000). After more than a century since they were effectively sterilised by volcanic activity, the Krakatau islands have a dramatically different termite fauna from the mainland (Abe 1984, Gathorne-Hardy *et al.* 2000), with no soil-nesters present (which dominate the mainland fauna (Abe 1984)), illustrating the slow and disjunct colonisation of termites.

Area

It is known that fragmentation adversely affects termites in South America, causing a change in feeding group composition. (De Souza and Brown 1994, Davies 2001). Soil feeding termites are less abundant in small forest fragments than large ones, perhaps because of their microclimate requirements (Davies in press). I do not have sufficiently accurate fragment size measurements of our study sites to evaluate the effects in Sundaland. Preliminary work in Sabah however, indicates that area might have an important effect on termite composition (Homathevi 1999).

Figure 6.4 Primary rainforest, Leuser Ecosystem. Sumatra.

Figure 6.5 Logged, burned and farmed land, two hours' drive from picture above. Leuser Ecosystem, Sumatra.

Conservation

If the object of conservation is only to maintain the current termite species checklist in the region, the outlook for termites is good. The termites of Sundaland are quite homogenous; most species are found in most parts of the region (chapter 5) and 83% of all Southeast Asian genera have been found in the protected regions of Sabah alone, or are ubiquitous, in the case of pests (Thapa, 1981, Thapa 1997, Eggleton *et al.* 1999). Therefore, to preserve most termite species of the region, one only needs to preserve a relatively small area of rainforest, about the size of the protected areas in Sabah (as long as this is large enough so that fragmentation and area effects do not cause species loss).

However, if the object of conservation is also to preserve fully functioning termite assemblages, and therefore the important ecosystem services that they provide, throughout the region, the situation is of great concern, as forest habitat suitable for termites is rapidly being lost. The number of monoculture plantations is increasing (in Indonesia, from 1982-1999 4.1 million ha of forest was converted to plantations) and is planned to increase further, especially as there is a growing demand for crude palm oil (Casson 2000). The huge fires of 1997-8 removed forest from large areas, and most forest in Sumatra and Kalimantan has been logged and is now fire-prone (Whitten *et al.* 2001, Jepson *et al.* 2001, Taylor *et al.* 1999).

If the removal of large areas of forest (for agriculture, plantations or by fire) continues, the diversity and abundance of termites in these areas will decline dramatically. If there are no nearby stands of undisturbed forest with a source of termites

to recolonise the cleared areas, it is possible that the termite composition and abundance (with their associated ecosystem services) will be affected for millennia.

However, with termites, as long as disturbance is not uniform over large areas, and if disturbed areas are left long enough, recovery is possible. If political action can be taken to protect National Parks, prevent fires and conversion of forest land to other uses, the termite-mediated functional processes and associated soil fertility may be able to be maintained in primary and selectively logged forests.

SYNTHESIS

7.1 Introduction

The earlier chapters of this thesis have focussed on different aspects of termite ecology, taxonomy, history and conservation. In this chapter I bring together the findings from these chapters, and synthesise them into an overview of the biogeography and ecology of Southeast Asian termites in the context of current events in the region.

7.2 Taxonomy

In order to do the ecological and biogeographical work described in this thesis, it was necessary to make several taxonomic decisions. Many groups (especially the soil feeding Nasutitermitinae and the *Termes/Capritermes* group) were in a state of some confusion. Many species had been inadequately described, the keys (where they existed) were difficult to use, and few synonymies had accompanied the descriptions. It was therefore almost impossible to correctly identify specimens from these groups, especially as the range of intra-specific and intra-colony variation had not been appreciated. Having access to a very large collection I was therefore able to confidently synonomise five genera and 17 species (I also discovered and described three new species). These taxonomic changes have enabled me to have confidence in the species assignations that I have used in my ecological work.

7.3 Biogeography and ecology.

Studies of the re-colonisation of Krakatau by termites have concluded that only termites that are able to raft can cross significant water gaps and colonise islands (Abe 1984, Gathorne-Hardy *et al.* 2000). However, termites have only had little more than a century in which to re-colonise the Krakatau islands, giving rise to the possibility that flying colonists, though they may have a high extinction rate upon arrival (Gathorne-Hardy *et al.* 2000) may be able to become established over several millennia or millions of years.

Sulawesi, which has presented a colonisation opportunity to termites for millions of years, shows that winged colonisation by obligate soil-nesters is very rare. Only one genus of this type of termite is present on Sulawesi (*Odontotermes*) and the species now found there are probably the descendants of a single colonising pair (Chapter 2). Otherwise, only termites which are able to raft have colonised the island. These termites have not evolved into any new genus, showing that they have a relatively slow rate of evolution. The Sulawesi study shows that a large part of the termite assemblage (the soil-nesters) cannot cross water gaps, even after millions of years.

Termites are not only severely limited by water gaps; altitude also affects their species richness, abundance and composition (Chapter 3). Altitude affects all termites (species richness declines with even a hundred metre increase in altitude) but affects the feeding groups differently. Group II termites, which are obligate foragers, are energetically the least able to survive the harsher conditions up mountains. This is because foraging requires too much energy to be a sustainable practice at high altitudes. However, by about 1800 or 2000 m a.s.l. all feeding

grouns are so affected by the harsh climate that no termite is found (Chapter 3, Collins 1980).

Local climate differences, even quite small ones, can affect termite assemblage and composition. Differences in rainfall across the Leuser ecosystem cause the Macrotermitinae to have a higher relative abundance in the drier, eastern part (they are at a competitive advantage over other group II feeders in drier areas) than the western, wetter side (Chapter 3).

Disturbance too affects termites, reducing their species richness and relative abundance and also changing the composition (Chapters 3 and 6). Termites are very much affected if the canopy is opened or removed, especially soil feeders. These termites are thought to live on an energetic knife edge (Davies *et al.* 1998, Jones 2000, Davies 2001, Chapter 6) and are pushed to the lower limit of energetic viability due to the greater diurnal temperature and moisture fluctuations in opened forest.

It has been proposed that the effects of Quaternary climate change (when most of the region was covered by savannah vegetation and rainforest was confined to a few refugia) could explain present day distributions of birds (Medway 1972) and primates (Brandon-Jones 1998) and many other mammals (Cranbrook 2000). However, the geographical extent of Quaternary vegetation change was unknown, so these suggestions remained untested.

The data from chapters two and three, as well as published and unpublished research, show that most termites tend to be poor dispersers–they cannot cross the sea or mountain ranges (Chapters 2 and 3, Abe 1984, Collins 1980, Gathorne-Hardy *et al.* 2000), and are generally poor fliers (Nutting 1969). Termite assemblages are affected by differences in rainfall patterns (Chapter 3

[redacted]mposition changes and species richness declines if the canopy is opened (Dibog *et al.* 1999, Jones 2000, Chapter 3). From these findings I was able to form the hypothesis that present day termite assemblage data would be able to show the extent of the Quaternary rainforest refugia.

Having transect data from throughout the region, I was able to test this hypothesis against palynological, fossil and geological data, and to demonstrate that termites could act as Quaternary rainforest indicators. I then used all termite data from the region to elucidate the extent of these rainforest refugia.

During the ice ages, when the climate became more seasonal, rainforest refugia existed in the Mentawai islands, most of the north of Sumatra and the base of the Barisan mountains. Northern Sarawak, Brunei, Sabah and eastern Kalimantan up to the Barito river were also refugia. Thailand, the Malay Peninsula, southeast Sumatra, western Borneo (west of the Barito and Lupar rivers) and Java were severely affected by Pleistocene drought, and were covered by savannah vegetation (Chapter 5). The map on page 135 illustrates the extent of the rainforest refugia.

Although differences in the termite assemblages in Southeast Asia can be explained by local, ecological or geographical factors (see Chapter 3, Jones 2000, Jones & Prasetyo in press), at the regional level, it is historical factors that best explain the different assemblage structures (Chapter 5). This has also been found to be true on the global scale (Davies 2001). It has become apparent that on an evolutionary time-scale, the rainforests of Java, Sumatra, Borneo and the Malay peninsula are part of one land mass, periodically flooded and with constantly changing vegetation types, with savannah and rainforest alternately advancing and

contracting. Understanding the effects of past environments may well provide explanations for the distribution, evolution and ecology of organisms other than termites, such as trees (Morley 2000), birds (Medway 1972, Cranbrook 2000), primates (Brandon-Jones 1996, 1998) and potentially many others.

Knowing the sites of the refugia also has important conservation implications. It is probable that the rainforest refugia are centres of speciation, not because of their fragmentation and subsequent isolation from each other, but because of their long-term stability, allowing fragile organisms (such as soil-feeding termites) to persist. The recognition of the refugia sites, and that recovery from prehistoric disturbance is still not complete, highlights the long-term fragility of the rainforest ecosystem and the importance of conserving prehistoric refugia as modern rainforest refugia, or national parks (Chapter 5).

One of the most striking features about conducting research in Sundaland is how little primary rainforest is left in the region. Probably less than 8% of Sundaland's primary forest remains (Myers *et al.* 2000) and it is estimated that Sumatra will have no primary forest by 2005 and Kalimantan none by 2010 (Jepson *et al.* 2001). Forest fires, conversion to large-scale agriculture and illegal logging continue (Jakarta Post, personal observations), especially now that law and order have broken down in Indonesia.

Having a dataset of transect data from the whole region, including sites which have been heavily disturbed, I was able to analyse the effects of different types of disturbance on termite assemblages (chapter 6). The discovery that turnover is very low across the region meant that I could compare sites directly without reference to the site's location. This was very helpful, as it enabled me to

examine the effects of more types of disturbance than one is likely to find in a single site.

Termites (and their important ecosystem services) are severely affected by removal of the rainforest canopy (chapter 6, Dibog *et al.* 1999). Although the assemblage can recover fully within 60 years if an undisturbed source area is nearby (chapter 6), over larger areas of hundreds of kilometres it is likely that the assemblage will take millennia to recover, and severely disturbed islands may not recover their assemblages while they remain islands (chapter 6).

With this huge amount of disturbance, National Parks are increasingly valuable to act as modern rainforest refugia. However, many National Parks are being entered and illegally logged (Jepson *et al.* 2001, personal observations) or the land used for agriculture (personal observations). The design and position of National Parks often makes them less effective as conservation areas. Many of the larger national parks in Sundaland are sited around mountains (Gunung Leuser, Kerinci-Seblat, Bukit Barisan Selatan, Gunung Palung, Bukit Raya, Kayan-Mentarang, Gunung Mulu, Gunung Kinabalu, Gunung Gede-Panggangro, Gunung Halimun), with only the edges having lowland forest. In termites, and many other organisms, species richness and abundance decline with altitude (chapter 3, Collins 1980, Olsen 1994, MacKinnon *et al.* 1997). Mountains contain a large number of endemics (MacKinnon *et al.* 1997) but lowland forest has far more species and is under greater pressure from exploitation for its valuable timber and farmland. In the current state of disorder, with the national parks inadequately guarded, the edges tend to be exploited, leaving only the more mountainous interior pristine. As an example, the Gunung Leuser National Park in northern Sumatra is a Quaternary rainforest refugium (chapter 5) and is one of the last areas

in the world where elephants, tigers, rhinoceros, orang utan and clouded leopards all occur in the same ecosystem. Only 30% of its land area is below 1000 m (de Wilde & Duyfjes 1996) although a majority of the species found in the park are predominantly lowland species. This lowland forest is under great threat, much of it has been (and is being) logged or used for agriculture (personal observation, Syaukani pers. comm. van Schaik *et al.* 2001), reducing the lowland habitat to a very small area. The National Park is in danger of losing most of its species.

For termites and other predominantly lowland organisms, more areas of protected (and properly guarded) lowlands are needed. However, these should not be just in any lowland area, but particularly in quaternary rainforest refugia, which have an especially high conservation value (Chapter 5).

7.4 Future work

The termites of Southeast Asia are taxonomically the best known of the three main tropical regions (Eggleton 2000). However, the nomenclature is in great disorder, understanding of the phylogenetics of the region's termites is very sketchy and identification of specimens to species level is almost impossible for the non-expert.

Proper, systematic revision of the termites of Southeast Asia is needed, and now is the perfect time for this. The Natural History Museum has probably the best collection of Southeast Asian termites in the world. Never before has there been such an extensive and complete collection of termites from that region. These have been collected from many diverse sites, and include most named species and many unnamed ones. The series are generally quite long, with 10-20 specimens from each colony, giving a clear idea of intra-colony variation (often

underestimated before, see chapter 3). At least 3000 series have been collected (into 80 or 90% ethanol) in the past four years. Much of the DNA has not yet become degraded, so an opportunity for using molecular techniques to analyse termite systematics exists.

If morphological and molecular methods could be combined a very much clearer picture of termite systematics would emerge, particularly with relation to species definitions, reliable morphological characters and an overall phylogeny. This in turn would greatly help us to understand the colonisation history of the region's termites.

In this thesis, I have shown that analysing termite data at the Functional taxonomic group (FTG) level gives clear and usable results. Although not all of the FTGs are taxonomically "real" (some of them may be paraphyletic groups) they are still a very useful ecological tool. In many cases, FTG analysis has proved to be more useful than species level analysis (chapters 5 and 6).

Identification is much easier and faster (the taxonomist has to learn only nine "taxa" rather than the 300 or so species and morphospecies found in the region). Identifying termites to the FTG level removes one of the major obstacles to termite study in Sundaland. Collecting termites in an effective, standardised manner is easy with the transect method of Jones & Eggleton (2000), but the major bottleneck has been identifying the collected specimens. This is time-consuming, even for an expert (Jones & Eggleton 2000), and is an extremely daunting task for a Sundan researcher who may well lack the expertise, reference collections and time to identify termites to species. Analysing data at FTG level minimises the effects of possible alpha-taxonomic mistakes and species patchiness (Chapter 5). Although the transect method is an efficient way of sampling

termites, only about 35% of the local species pool is sampled in any one transect (Jones & Eggleton 2000). This means that unless strong environmental factors are being investigated, pseudoturnover dampens the signal shown by the data. Therefore, analysis at FTG level (which has very little pseudoturnover) is appropriate when examining many environmental effects. Identifying the termites to FTG level makes termite research much easier and more accessible, without removing the scientific integrity of the results.

In Indonesia (home to most of the Southeast Asian Quaternary rainforest refugia) fires have destroyed more than 10% of the land area of Sumatra and Borneo in the past 20 years (Taylor *et al.* 1999, Whitmore 1999). Almost all of the lowland forest in Sumatra and Kalimantan is expected to be disturbed by 2010 (Jepson *et al.* 2001) and disturbed forest is more fire-prone than primary (Taylor *et al.* 1999). ENSO events (causing drought in the region) are likely to increase in the future (Walsh & Newberry 1999), also making more forest fires likely, as does the continuing lack of law and order.

I have already shown that termites are greatly affected when the forest canopy is removed and have hypothesised that over long distances it will take millennia for the composition to recover (chapter 6). I have also shown that the termite assemblage can recover completely in less than 60 years in secondary forest. This shows that for termites at least, secondary forest has a high conservation value.

Termites, although they are key decomposers, are only a small part of the soil fauna. Beetles, ants, earthworms, woodlice, millipedes and spiders are all abundant and extremely important, as "ecosystem engineers" and as providers of "ecosystem services" (Lavelle *et al.* 1997).

Research into the effects of burning on these soil macrofauna, and investigating their rates of recovery over long and short distances will give us valuable information about the long- and short-term environmental impact of the forest fires. In order to assess damage and where conservation effort should be targeted, the patterns of recovery and interactions of the soil macrofauna and their ecosystem services must be understood.

Appendix 6.1 Species level data used in chapters 5 and 6

	CODE	ThKhSo	ThDoSuFP	ThDoSuB	ThKhYa	PMPas1	SaDanYSF1	SaDanYSF2	SaDanOSF1	SaDanOSF2	SaDanPF1	SaDanPF2	BU1ry	BU2ndry	GP	Tabysf	Tabosf	TabGnem	SuKet500	SuSuaq	SuMRT	SuBuLaw1	SuBuLaw2	SuLokop	SuJaPF	SuJaLogF	SuJaJR	SuJaRP	SuJaPar	SuJaI	SuJaC	SuWK	BBar	SibT1	SibT2	JaUjKuln	JaPangl1	JaPangl2
	FOREST TYPE	Secondary	Fire-protected	Burnt	Primary dry evergreen	Primary rainforest	(3yo) young logged forest 1	(3yo) young logged forest 2	(18 yo) Old logged forest 1	(18yo) Old logged forest 2	Primary rainforest 1	Primary rainforest 2	Primary rainforest	57-year-old secondary forest	Primary rainforest	(2yo) young logged forest	(15 yo) old logged forest	*Gmelina arborea* plantation	Ketambe 500 m primary forest	Suaq	MRT	Bukit Lawang 350 m	Bukit Lawang 250 m	Lokop	Primary rainforest	Logged forest	Jungle rubber	Rubber plantation	*Paraserianthes falcata* plantation	*Imperata* field	Cassava field	Primary rainforest (flooded)	Primary rainforest	Primary rainforest	Primary rainforest	Primary rainforest	(*c.* 70 yo) Secondary forest 1	(*c.* 70 yo) Secondary forest 2
	SITE	Thailand Khao Sok	Thailand Doi Suthep-Pui	Thailand Doi Suthep-Pui	Thailand Khao Yai	Malay peninsula Pasoh	Borneo Danum	Borneo Danum	Borneo Danum	Borneo Danum	Borneo Danum	Borneo Danum	Borneo Barito Ulu	Borneo Barito Ulu	Borneo Gunung Palung National Park	Borneo Tabalong district	Borneo Tabalong district	Borneo Tabalong district	Sumatra Leuser Ecosystem primary forest	Sumatra Leuser Ecosystem primary forest	Sumatra Leuser Ecosystem primary forest	Sumatra Leuser Ecosystem primary forest	Sumatra Leuser Ecosystem primary forest	Sumatra Leuser Ecosystem primary forest	Sumatra Jambi study site	Sumatra Jambi study site	Sumatra Jambi study site	Sumatra Jambi study site	Sumatra Jambi study site	Sumatra Jambi study site	Sumatra Jambi study site	Sumatra Way Kambas National park	Sumatra Bukit Barisan Selatan National park	Siberut	Siberut	Java Ujung Kulon national Park	Java Pangandaran Nature Reserve	Java Pangandaran Nature Reserve
Glyptotermes	*pinangae*	2																																				
Glyptotermes	*paracaudomunitus*								1																													
Glyptotermes	*brevicaudatus*								1																													
Glyptotermes	*paratuberculatus*																							1														
Glyptotermes	*sp B*										1																	1										
Neotermes	*tectonae*																																				1	
Neotermes	*sp A*				1																																	
Cryptotermes	*sp nov 1*																							1														
Cryptotermes	*sp*																					1																
Heterotermes	*tenuior*						3	5	9	3	4	5	11	5		1				2					1													
Parrhinotermes	*minor*					1								1			1										1											
Parrhinotermes	*pygmaeus*					1							2							2		2												2				
Parrhinotermes	*buttel-reepeni*																			1																		
Parrhinotermes	*aequalis*							1	1				1		1					1	2	2	2	2									1					
Parrhinotermes	*nr sp. C*																									1												
Parrhinotermes	*microdentiformis*					1									1				1	1		1		1														
Parrhinotermes	*microdentiformisoides*																				1																	
Coptotermes	*kalshoveni*																						1									1						
Coptotermes	*sepangensis*								2	2							5					1							4									
Coptotermes	*borneensis*																							1					1									

		ThKhSo	ThDoSuFP	ThDoSuB	ThKhYa	PMPas1	SaDanYSF1	SaDanYSF2	SaDanOSF1	SaDanOSF2	SaDanPF1	SaDanPF2	BU1ry	BU2ndry	GP	Tabysf	Tabosf	TabGnem	SuKet500	SuSuaq	SuMRT	SuBuLaw1	SuBuLaw2	SuLokop	SuJaPF	SuJaLogF	SuJaJR	SuJaRP	SuJaPar	SuJal	SuJaC	SuWK	BBar	SibT1	SibT2	JaUjKuln	JaPangl1	JaPangl2
Coptotermes	*curvignathus*										2									1					1	1	1	3	1									
Schedorhinotermes	*sp. A*	3																																			
Schedorhinotermes	*sp. B*	1																																			
Schedorhinotermes	*nr. rectangularis*				1																							9									
Schedorhinotermes	*sarawakensis*		1					3			1	3					1	2			2			2	1						2						
Schedorhinotermes	*brevialatus*						1	1	1	2			1	2		1	1	1										3			1						
Schedorhinotermes	*medioobscurus*					4	6	3	4	2		1	7	7	5	14	1	14	3	9	8	8	9	5	7	7	10		7				6	6	2	4	1	
Schedorhinotermes	*malaccensis*												1																								
Reticulitermes	*sp. A*				4																																
Termitogeton	*planus*																						1														
Macrotermes	*annandalei*		4		10																																
Macrotermes	*gilvus*	1							1	5						4	2													1	1	3			8	5	9
Macrotermes	*malaccensis*	2				10	3	1		4	6	1	3		1	6	6		8	6	6	2		3								10					
Macrotermes	*ahmadi*																			1		2			1												
Odontotermes	*proformosanus*			3																																	
Odontotermes	*formosanus*			1																																	
Odontotermes	*feae*			1																																	
Odontotermes	*nr. obesus*				7																																
Odontotermes	*nr. takensis*	1																																			
Odontotermes	*sp. A*	3																																			
Odontotermes	*sp. B*	3																																			
Odontotermes	*denticulatus*					3										1											5										
Odontotermes	*neodenticulatus*															2																					
Odontotermes	*grandiceps*					3															1														1		3
Odontotermes	*oblongatus*					2	2	2		2	2				2				2				3														
Odontotermes	*sarawakensis*					9	1		6	4	5	4				13	4		1	6	6				10	9						12					
Odontotermes	*sp. C*								1	1																											
Odontotermes	*sp. D*					4			0																												
Odontotermes	*minutus*												5	11					1	1	3										3				4		
Odontotermes	*javanicus*																															2	1		1	1	1
Odontotermes	*sp. 1*																			2																	
Odontotermes	*billitoni*																															1	1		6		4
Hypotermes	*xenotermitis*	3	2	2			4	4	2	1							1																1	3			
Ancistrotermes	*pakistanicus*		5	6		3												7								3								18	9	9
Microtermes	*obesi*			4																																	
Labritermes	*emersoni*					1				1												1			1												
Labritermes	*buttel-reepeni*													3						2			1				1	2									
Labritermes	*kistneri*											3		2	1							3	2	1													
Amitermes	*dentatus*																						1														
Microcerotermes	*minutus*		3																																		
Microcerotermes	*crassus*		11	10																																	
Microcerotermes	*paracelebensis*	3																																			

		ThKhSo	ThDoSuFP	ThDoSuB	ThKhYa	PMPas1	SaDanYSF1	SaDanYSF2	SaDanOSF1	SaDanOSF2	SaDanPF1	SaDanPF2	BU1ry	BU2ndry	GP	Tabysf	Tabosf	TabGnem	SuKet500	SuSuaq	SuMRT	SuBuLaw1	SuBuLaw2	SuLokop	SuJaPF	SuJaLogF	SuJaJR	SuJaRP	SuJaPar	SuJaI	SuJaC	SuWK	BBar	SibT1	SibT2	JaUjKuIn	JaPangl1	JaPangl2
Microcerotermes	*dubius*					2			2	1		1				4	3																					
Microcerotermes	*serrula*						1	3	6	5	12	1	2			4	5			2	2	1	1	5	3	7		1						2	2			
Mictocerotermes	*sp 1*																														1					1	1
Microcerotermes	*nr. havilandi*														2										1												
Globitermes	*sulphureus*	2	2	1	2																																
Globitermes	*globosus*						3			4	1	11		3	3	3	4			8	8				8	4	1			4			9				
Prohamitermes	*mirabilis*					1	2	1	4	4		2	3	3	1	8	3				5	15	13	4	3	7		6	4									
Prohamitermes	*sp. 1*											1																									
Protohamitermes	*globiceps*																1																				
Termes	*propinquus*											1				4				2	1		4		3			12	1								
Termes	*lacticornis*																																1				
Termes	*comis*																1								4	1			1					1	1		
Termes	*borneensis*							5					2																				1				
Pericapritermes	*sp. A*	3																																			
Pericapritermes	*sp. A*				1																																
Pericapritermes	*sp. B*				1																																
Pericapritermes	*sp. C*				1																																
Pericapritermes	*nitobei*					1	3		3	9	2	2	5	1	2	2	1			2	2	1	2	4	1		2					3	10	6	3		
Pericapritermes	*sp. C*					1	3	3	2	3	1	5																									
Pericapritermes	*latignathus*																5				1												14	12	11	4		1
Pericapritermes	*sp.D*																			10		2	3	8													
Pericapritermes	*sp.4*																			2																	
Pericapritermes	*semarangi*						4	2	3	3	8	6								6	1		3	6	2					5							
Pericapritermes	*sp. A*							1		2	2	1								2	1												3				
Pericapritermes	*sp. B*												1																								
Pericapritermes	*sp.8*																				1			1													
Pericapritermes	*buttenzorgi*																																			1	2	3
Pericapritermes	*nr. dolichocephalus*						2	2	5			1	4														6				3	3		1			
Procapritermes	*setiger*																								8	6	2										
Procapritermes	*minutus*							2		1	2	2	1												4		1										
Procapritermes	*prosetiger*	2								2	2	1		1	3	11	7								3	2	10						5	4			
Procapritermes	*nr. sandakanensis*						1	5	3	3	2	1																									
Procapritermes	*atypus*															1	1																				
Procapritermes	*sp. A*				2																																
Procapritermes	*sp.B*				1																																
Procapritermes	*sp. C*				3																																
Procapritermes	*?neosetiger*					1	1	4									3											6									
Procapritermes	*sp. A*						3	1			1	3	2															5									
Procapritermes	*sp. B*										2	4	3							2	8	1	3														
Procapritermes	*sp. C*									1		4	1																								
Procapritermes	*sp. E (? = P. neosetiger)*									3	7	7	6																								
Procapritermes	*spF*																1																				

		ThKhSo	ThDoSuFP	ThDoSuB	ThKhYa	PMPas1	SaDanYSF1	SaDanYSF2	SaDanOSF1	SaDanOSF2	SaDanPF1	SaDanPF2	BU1ry	BU2ndry	GP	Tabysf	Tabosf	TabGnem	SuKet500	SuSuaq	SuMRT	SuBuLaw1	SuBuLaw2	SuLokop	SuJaPF	SuJaLogF	SuJaJR	SuJaRP	SuJaPar	SuJal	SuJaC	SuWK	BBar	SibT1	SibT2	JaUjKuln	JaPangl1	JaPangl2
Procapritermes	*sp. 1*																		5	1	2																
Procapritermes	*sp. 2*																						1														
Pseudocapritermes	*sp. 3*																							1													
Pseudocapritermes	*silvaticus*																3																				
Pseudocapritermes	*sp. 1*												3	9																							
Pseudocapritermes	*orientalis*					4					1	1				3	1		1	4	2		5	2	8	5	2						6	15	11			
Mirocapritermes	*concaveus*			1	1											2	1																			
Mirocapritermes	*nr. latignathus*	1																																			
Mirocapritermes	*connectens*						2	1	1	6	3	4	1	4											2							1					
Dicuspiditermes	*garthwaitei*		4	4																																	
Dicuspiditermes	*nemorosus*					4			1	1			7	1	5	4				1	1	6	5	2	14	18	12	13	2			8	13	3	4			
Kemneritermes	*sarawakensis*					1							1			1						10			4	1											
Homallotermes	*eleanorae*													1		2			1						1			3									
Homallotermes	*exiguus*										1			2	4									1													
Homallotermes	*foraminifer*																								1	4											
Syncapritermes	*sp. A*							2																													
Orientcapritermes	*sp. A*								2	3	2	5																									
Orientcapritermes	*kluangensis*					3							3	1																							
Gen. Nov	*sp. Nov*								2																												
Speculitermes	*rongrensis*		2	4																																	
Euhamitermes	*sp. A*		4	1																																	
Euhamitermes	*sp. C*					1																															
Euhamitermes	*sp*							2	2			1					2															2				1		
Euhamitermes	*sp. 2*						2				1																										
Euhamitermes	*sp. 3*						3					1																									
Lacessititermes	*pilferus*																							1													
Lacessititermes	*lacesstitus (sp C')*																															3				2	
Hospitalitermes	*ataramensis*	1																																			
Hospitalitermes	*umbrinus*																							6													
Hospitalitermes	*hospitalis*						2							1		4	1								4			2				1			1			
Longipeditermes	*longipes*			1			1				1		2	4		2			5	6	4	3	2	4									4				
Havilanditermes	*atripennis*							2			1																										
Nasutitermes	*johoricus*	11																															1				
Nasutitermes	*matangensiformis*				1																																
Nasutitermes	*sp. A*							3																													
Nasutitermes	*longinasus*					2	2		1			4				4					3		2											1			
Nasutitermes	*longirostris*															1																					
Nasutitermes	*matangensis*	1						1					3			1										2						1	4	1	2	1	1	
Nasutitermes	*acutus*																																			1	1
Nasutitermes	*longinasoides*																		3																		
Nasutitermes	*sp B*						1												2																		
Nasutitermes	*Sp C*																											2									

		ThKhSo	ThDoSuFP	ThDoSuB	ThKhYa	PMPas1	SaDanYSF1	SaDanYSF2	SaDanOSF1	SaDanOSF2	SaDanPF1	SaDanPF2	BU1ry	BU2ndry	GP	Tabysf	Tabosf	TabGnem	SuKet500	SuSuaq	SuMRT	SuBuLaw1	SuBuLaw2	SuLokop	SuJaPF	SuJaLogF	SuJaJR	SuJaRP	SuJaPar	SuJaI	SuJaC	SuWK	BBar	SibT1	SibT2	JaUjKuln	JaPangl1	JaPangl2
Nasutitermes	*Sp D*																											2									
Nasutitermes	*neoparvus*								1	2									2	1			3					1									
Nasutitermes	*havilandi*																								1		2		3									
Bulbitermes	*laticephalus*				4																																
Bulbitermes	*sp. C*									1		1																									
Bulbitermes	*singaporiensis*												4	3								9	8	2													
Bulbitermes	*flavicans*						1	5	3	1				5					1		1		1											2			
Bulbitermes	*borneensis*																															4	5	4			
Bulbitermes	*sp.1*																					10	13	13													
Bulbitermes	*constrictus*	1			1	1	8	3		7	1	3	7	3					10	12	7	5	2	12	3	1					7	12	9	13	1	1	7
Bulbitermes	*germanus*																								2												
Bulbitermes	*prabhae*																								1												
Hirtitermes	*hirtiventris*																						1														
Hirtitermes	*atripennis*																		1																		
Hirtitermes	*spinocephalus*								1																												
Hirtitermes	*brabazoni*												1	3																							
Ceylonitermes	*indicola*																							3										3			
Acticulitermes	*maymyoensis*				1																																
Orientsubulitermes	*inanis*					1													2	7	9	4	4	2	2	4	2						2				
Subulioditermes	*sp. A*						2																														
Subulioditermes	*sp.D*					1																															
Sabahitermes	*leuserensis*																		2					1													
Malaysiotermes	*spinocephalus*					2	4	1	2	4	6	4	8	9		1			3	3		1	3	4	1	3						1	10	15	3		
Malaysiotermes	*holmgreni*												4	2										1	2	3											
Leucopitermes	*leucops*															1	1			1	1			1	1												
Leucopitermes	*sp. Nov*					1													2						1							1					
Gen et sp. Nov 1																1																					

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